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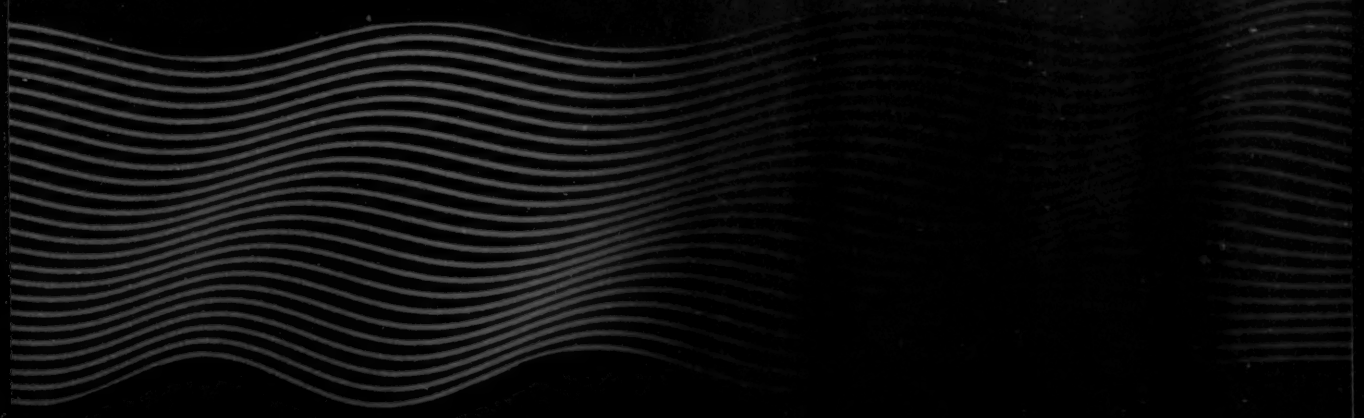
Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques



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The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy: The Journal publishes original research articles, perspectives (syntheses, critiques, re-evaluations), discussions (comment and reply), and rapid communications. Manuscripts may concern cells, organisms, populations, communities, ecosystems, or processes that affect aquatic systems. They may cover a range of disciplines including biology and ecology of marine and freshwater organisms, limnology, oceanography, physiology, toxicology, genetics, economics, disease, and management. Preference will be given to manuscripts that emphasize understanding of observed phenomena and interpretation of experimental results. The Journal encourages papers that lead from clearly stated purpose or rationale and from testable hypotheses, concepts, or questions to identifiable conclusions or syntheses. Such papers may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of aquatic sciences. The Journal discourages papers that are essentially descriptive, except in emerging disciplines; have only site-specific or local applications (a certain year, place, taxon, chemical compound, etc.); only confirm previously established principles; or apply standard techniques without breaking new methodological ground.

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Aucun remboursement ne sera accordé ni aucune annulation acceptée une fois que les livraisons auront commencé. Les réclamations de numéros manquants devront être soumises dans les quatre mois (Amérique du Nord) ou dans les six mois (à l'extérieur de l'Amérique du Nord) suivant la date de publication. L'éditeur ne fournira de numéros manquants que si le document a été perdu pendant l'expédition et que si le stock le permet. Adressez tout changement d'adresse ou toute question quant à l'abonnement au : Bureau des abonnements, Presses scientifiques du CNRC, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada; téléphone : 613-993-9084; télécopieur : 613-952-7656; adresse électronique : research.journals@nrc.ca.

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CJFAS has had a long tradition of publishing the proceedings of symposia in special issues and supplements of the Journal. We would like to inform our readers that this practice has not changed and to remind you of the basic guidelines for the publication of these collections of manuscripts.

Organizers of symposia should contact the Editors well in advance of the symposium date, detailing such information as the theme and scope of the symposium, as well as the expected number of contributions. A typical supplement contains 20–25 manuscripts, though larger groups of papers are acceptable. Proceedings based on fewer papers may be published as a group, along with other peer-reviewed manuscripts, in a regular issue of the Journal. Once the Editors are in general agreement that the collection of manuscripts meets CJFAS Editorial policy, symposia organizers will need to make financial arrangements with NRC Research Press. Depending upon the subject and deemed importance to the readers of CJFAS, there may be an opportunity to waive page charges partially or in entirety.

Symposium proceedings are peer reviewed with the same degree of rigor as regular Journal submissions. For groups of papers greater than 10–12, a common practice is to invite the symposia organizers to act as Guest Associate Editors during the review process. The Journal office typically handles the initial stages of the review process involving the acquisition of reviews. Although Guest Associate Editors are required to suggest the names of 2–3 potential referees per manuscript, the final selection of referees remains with the Editors. Guest Associate Editors will be asked to evaluate the reviews of each manuscript and make any additional comments, as they deem necessary. This evaluation of reviews includes the arbitration of divergent reviews, should the referees differ in their opinion of a particular manuscript. After peer review has been completed, the Guest Associate Editors are asked to correspond directly with the authors, and they are responsible for the coordination of revisions. Only when the manuscript is in final, publishable form do they return the works to the Editorial office.

For further details on CJFAS supplements and special issues, and for a complete set of guidelines, please contact the Editorial office.

Telephone: (519) 824-4120, extension 2646
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La publication de numéros spéciaux et de suppléments

Le JCSHA a l'habitude de publier les actes des symposiums dans des numéros spéciaux et des suppléments. Nous voulons aviser nos lecteurs que cette pratiqué n'a pas changé et vous rappeler les lignes directrices de base concernant la publication de cette collection de manuscrits.

On demande aux organisateurs du symposium de communiquer avec les éditeurs bien avant la tenue du symposium, afin de les informer du thème et de la portée de celui-ci, ainsi que du nombre de communications prévues. Habituellement, un supplément contient de 20 à 25 manuscrits, mais il est possible d'augmenter ce nombre. On peut regrouper un plus petit nombre de manuscrits et les publier avec d'autres manuscrits examinés par les pairs dans un numéro ordinaire. Quand les éditeurs conviennent que les manuscrits correspondent à la politique éditoriale du JCSHA, les organisateurs du symposium doivent conclure un accord financier avec les Presses scientifiques du CNRC. Selon le sujet et son importance pour les lecteurs du JCSHA, on pourra supprimer partiellement ou entièrement les coûts par page.

Les actes du symposium sont examinés par les pairs aussi rigoureusement que le sont les autres textes soumis au Journal à des fins de publication. Lorsque le nombre de communications groupées dépasse 10 ou 12, on invite habituellement les organisateurs du symposium à jouer le rôle de rédacteur adjoint invité pendant l'examen. Le Journal s'occupe des premières phases du processus, liées à la réalisation des examens. On demande aux rédacteurs adjoints invités de suggérer le nom de deux ou trois lecteurs par manuscrit, mais le choix final des lecteurs revient aux éditeurs. Les rédacteurs adjoints invités devront évaluer les examens effectués pour chaque manuscrit et faire des commentaires supplémentaires s'il le juge nécessaire. L'évaluation des examens comprend l'arbitrage des divergences lorsque les lecteurs n'ont pas la même opinion au sujet d'un manuscrit. Quand l'examen par les pairs est terminé, les rédacteurs adjoint invités communiquent directement avec les auteurs et coordonnent l'apport des corrections. Ils ne remettront au bureau de la rédaction que la version finale des manuscrits, prête à être publiée.

Pour avoir des renseignements supplémentaires sur les numéros spéciaux et les suppléments du JCSHA ou pour obtenir les lignes directries complètes, veuillez communiquer avec le bureau de la rédaction.

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http://www2.ucsc.edu/people/msmangel/Krill_Symposium.html

The Second International Symposium on Krill

We are pleased to announce the Second International Symposium on Krill, **23–27 August 1999** on the campus of the University of California Santa Cruz.

The purpose of this symposium is to review current knowledge of krill euphausiid biology, to highlight gaps and future areas for research, and to show how the study of a range species of krill can illuminate more general problems (for example, krill flux, recruitment, swarming behaviour, age, and growth). The sessions (and invited speakers) are

- **Krill demography, life history, and genetic diversity** (V. Siegel, Germany; Vassily Spirodonov, Germany; T. Paternello, Italy; E. Pakamov, South Africa)
- **Krill development, growth, reproduction, and aging** (N. Iguchi, Japan; S. Nicol, Australia; J. Cuzin-Roudy, France)
- **Krill physiology, metabolism nutrition, and energetics** (L. Quetin, U.S.A.; F. Buchholz, Germany; R. Perissinoto, South Africa; Y. Nishino, Japan; P. Mayzaud, France; S. Falk-Petersen, Norway; A. Clarke, U.K.)
- **Krill behavior: swarming, vertical migration, foraging, and antipredator mechanisms** (W. Hamner, U.S.A.; D. Ritz, Australia; L. Madureira, Brazil; J Watkins, U.K.; A. Brierley, U.K.)

The opening talk will be given by D. Miller (South Africa).

Each day will include invited and contributed talks and poster sessions. Proceedings of the meeting will be published; contributors will be expected to arrive with disk and hard copies of their papers.

A call for contributed talks will occur in fall 1998. Special support will be available for young investigators and students.

Further communication will occur electronically, either at the web site **http://www2.ucsc.edu/people/msmangel/Krill_Symposium.html** or by contacting Marc Mangel by e-mail (msmangel@cats.ucsc.edu).

International Organizing Committee: Marc Mangel, Steve Nicol, Janine Cuzin-Roudy, Yoshi Endo, Denzil Miller, Robin Ross, Völker Siegel, and Jon Watkins

Local Host Committee: Sarah Barnett, Don Croll, Marc Mangel, and Baldo Marinovic

Le deuxième symposium international sur le krill

Nous sommes heureux d'annoncer la tenue du deuxième symposium international sur le krill, **du 23 au 27 août 1999,** sur le campus de l'Université de Californie, Santa Cruz.

Le symposium a pour objet d'examiner les connaissances actuelles sur la biologie du krill, de souligner les lacunes et les futurs sujets de recherche et de montrer comment l'étude de diverses espèces de krill peut éclairer des problèmes plus généraux (par exemple le flux, le recrutement, l'essaimage, l'âge et la croissance du krill). Voici les titres des exposés, accompagnés des noms des conférenciers invités.

- **Démographie, cycle biologique et diversité génétique du krill** (V. Siegel, Allemagne; Vassily Spirodonov, Allemagne; T. Paternello, Italie; E. Pakamov, Afrique du Sud)
- **Développement, croissance, reproduction et vieillissement du krill** (N. Iguchi, Japon; S. Nicol, Australie; J. Cuzin-Roudy, France)
- **Physiologie, métabolisme, nutrition et énergétique du krill** (L. Quetin, É.-U.; F. Buchholz, Allemagne; R. Perissinoto, Afrique du Sud; Y. Nishino, Japon; P. Mayzaud, France; S. Falk-Petersen, Norvège; A. Clarke, R.U.)
- **Comportement du krill: essaimage, migration verticale, quête de nourriture et protection contre les prédateurs** (W. Hamner, É.-U.; D. Ritz, Australie; L. Madureira, Brésil; J. Watkins, R.U.; A. Brierley, R.U.)

M. D. Miller (Afrique du Sud) prononcera le discours d'ouverture.

Des communications sollicitées, des communications offertes et des communications affichées seront présentées chaque jour. Les actes du symposium seront publiés; c'est pourquoi l'on demande aux conférenciers de copier leur communication sur disquette et sur copie papier.

À l'automne 1998, on lancera une invitation aux personnes intéressées à présenter des communications offertes. Un soutien spécial sera accordé aux jeunes chercheurs et aux étudiants.

À l'avenir, les renseignements seront transmis par voie électronique, soit par l'intermédiaire du site Web **http://www2.ucsc.edu/people/msmangel/Krill_Symposium.html** soit par courrier électronique (Marc Mangel : msmangel@cats.ucsc.edu).

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Bioenergetics and nitrogen balance of the European eel (*Anguilla anguilla*) fed at high and low ration levels

S.F. Owen, D.F. Houlihan, M.J. Rennie, and J.H. van Weerd

Abstract: European eel (*Anguilla anguilla*) were fed either high or low ration levels (1.33 and 0.48% body weight·day^{-1}). Eight periods of continuous 24-h respirometry in flow-through conditions were conducted over 70 days to simultaneously examine nitrogen and energy budgets without resorting to the calculation of parameters by difference. Food and oxygen consumption; ammonia, urea, and nitrate–nitrite excretion; and growth production were measured. Nitrogen budgets successfully accounted for 89.6–101.2% of the consumed nitrogen. Energy budgets accounted for 53.4–92.3% of the consumed energy. From the ammonia quotients (AQ), 54.4–57.7% of the available protein was oxidized at high ration, and 59.7–133.5%, at low ration level. To satisfy maintenance requirements, 0.28 mg N·g^{-1}·day^{-1} was required. At 25°C eels were calculated to have a rate of standard metabolism of 83.3 J·g^{-1}·day^{-1}, which is comparable with the range published for other species at this temperature. These data suggest that eels do not have a particularly low metabolic rate, as is commonly assumed in the eel rearing industry, and that the relatively inactive lifestyle associated with the eel masks a metabolic rate in common with other, more active, fish.

Résumé : Des anguilles d'Europe (*Anguilla anguilla*) ont été soumises à des rations alimentaires abondantes ou restreintes (1,33 et 0,48 % du poids corporel·jour^{-1}). Huit séances de respirométrie continue d'une durée de 24 h en écoulement continu ont été réalisées sur une période de 70 jours en vue d'examiner conjointement le bilan de l'azote et le bilan énergétique sans avoir à déduire les paramètres par calcul des différences. Les paramètres suivants ont été mesurés : consommation de nourriture et d'oxygène; excrétion d'ammoniac, d'urée et de nitrate/nitrite; et croissance. Le bilan de l'azote a expliqué 89,6–101,2 % de la consommation d'azote, et le bilan énergétique, 53,4–92,3 % de l'énergie consommée. À partir des quotients d'ammoniac (QA), 54,4–57,7 % des protéines disponibles ont été oxydées chez les anguilles ayant reçu des rations abondantes; ce pourcentage atteignait 59,7–133,5 % chez les anguilles soumises à un régime alimentaire restreint. Pour satisfaire aux exigences de la maintenance, un apport de 0,28 mg N·g^{-1}·jour^{-1} était nécessaire. À 25°C, on a calculé que les anguilles présentaient un métabolisme standard de 83,3 J·g^{-1}·jour^{-1}; cette valeur se compare à l'éventail des mesures publiées pour d'autres espèces de poissons à cette température. Ces données contredisent l'impression largement répandue dans le secteur de l'élevage d'anguilles selon laquelle les anguilles ont un métabolisme particulièrement lent et donnent à croire que le mode de vie relativement inactif des anguilles contribue à masquer une vitesse de métabolisme comparable à celle d'autres espèces de poissons plus actifs.

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Introduction

Growth rates in fish are indeterminate, exhibiting a plasticity that is the net result of the complex interactions between a number of abiotic and biotic factors (Brett 1979). The study of bioenergetics, or physiological energetics as defined by Brett and Groves (1979), provides a framework to model how these factors affect the energy intake, energy partitioning, and the resultant growth rates in fish (Adams and Breck 1990). Food availability, whether food abundance in the wild or ration size offered to fish under culture conditions, can have a great influence on the potential for growth. The interaction between the level of energy intake and factors such as temperature, stress, and age will then determine the partitioning of the ingested energy between metabolism, activity, and growth (Cui and Wootton 1988*a*, 1988*b*). Car-

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nivorous fish utilize proteins as their primary energy source (van Waarde 1983); therefore, examining the metabolism and utilization of protein (and therefore nitrogen) will be an integral part of the study of bioenergetics in these species. The flow of energy derived from protein, lipid, and carbohydrate through an organism, as the proportions utilized in the energetic costs of growth and respiration, can be estimated via an energy budget (Brett and Groves 1979).

Few accounts have been published that simultaneously examine energy and nitrogen (N) budgets of fish, and those that do rarely measure all components, generally calculating one by difference (Jobling 1993). Brett and Groves (1979) have provided an excellent overview of some of the earlier investigations and suggest some composite budgets. More recent work concentrating on single species has been conducted and has given an insight into the relationship between energetics and nitrogenous flux (Cui and Wootton 1988*a*, 1988*c*; Carter and Brafield 1991, 1992; Xie and Sun 1993) and a comparison between species (Cui and Liu 1990*a*, 1990*b*, 1990*c*) for what can be generally regarded as active fish. However, recent work on postprandial snakes (Secor and Diamond 1997) has shown that low activity does not necessarily equate with a low metabolic rate.

The eel (*Anguilla anguilla*) is often regarded as a relatively sedentary species during its freshwater stages, and it is commonly assumed within the eel-rearing industry to have a correspondingly low rate of metabolism, although there are no evidence to support these beliefs. Further, the efficiency with which food is converted into body mass is generally lower in eels than, for example, in salmonids, which would suggest either less efficient feeding and digestion or the possibility of higher metabolic costs. The eel therefore offers the opportunity to examine the bioenergetics of a species possibly misconstrued as a low energy requiring fish and provides a model species to highlight the energy utilization in culture conditions.

This investigation was conducted to examine the effect of high and low ration level upon the energy utilization and protein growth of the eel and to construct a bioenergetic model at high and low energy intakes to provide the basic understanding of the protein utilization in culture by measuring all components of the budgets.

Materials and methods

Animals

The eels were obtained from a commercial growing-on farm (Vennendaal, the Netherlands) transferred to tanks at 25.7 ± 0.3°C and fed ad libitum for 1 h (12:00–13:00) daily for 12 days. The fish were treated on days 4 and 9 to reduce an infection of gill parasites (*Pseudodactylogyrus* spp.) using Mebenvit™ (5% Mebendazol) (Kortenoord, the Netherlands) at a dose of 6 $g \cdot m^{-3}$ for a 24-h exposure.

Two-hundred and thirty-five eels were divided equally between five respirometers. Three fish were taken from each respirometer for a representative initial body composition analysis, killed via an anaesthetic overdose (200 $mg \cdot L^{-1}$ Hypnodyl™; Janssen Pharmaceutical) and frozen at –26°C until analysis. The respirometry tanks were part of a 3000-L system of physically and biologically filtered recirculating water at 25 ± 0.8°C (mean ± SE) pH 7.4 ± 0.09 (values recorded at approximately 12:00 daily; $n = 70$) and a 12 h light : 12 h dark cycle (08:00–20:00) at the Department of Fish Culture and Fisheries, Wageningen Agricultural University, the Netherlands. The ration sizes of low ration (near maintenance) and high ration (near maximum) meal sizes were assigned to the five tanks. The groups of fish were hand fed (Provimi 2 mm Eel Grower, Provimi B.V., Rotterdam, the Netherlands) a calculated ration daily between 12:00 and 13:00, ensuring all pellets were eaten. Any uneaten pellets were counted and removed from faeces collectors. The total uneaten food each day was deducted from a formula of predicted daily weight increase, and the ration for each tank calculated daily to maintain the ration per unit weight of fish. The feed conversion factor of 1.6 was used to predict daily growth (Heinsbroek et al. 1991) and to calculate the daily ration. Low ration of the eel was taken to be 2.5 $g \cdot kg^{-0.8} \cdot day^{-1}$, and the high ration groups were fed at 8 $g \cdot kg^{-0.8} \cdot day^{-1}$ (grams food wet weight per kilogram fish live weight) (Heinsbroek et al. 1991).

Respirometry

Respirometry measurements were made over a 24-h period every 7 days for a total of 10 weeks (70 days), using automated continuous flow sampling. However, because of technical problems, 2 of the 10 recordings were removed from the data set. The respirometer was described by Heinsbroek et al. (1991). The eels were prevented from escaping from the respirometers via a 6-V DC current around the outlet. Faeces were separated continually, collected, and frozen every 8 h during the respirometry period. Any uneaten food pellets were easily separated from the faeces and deducted from the consumption. An acrylic lid excluded air from the respirometer.

Computer-controlled switching of magnetic valves allowed automated sampling of each respirometer every 5 min, as well as inflowing recirculated water. By this sampling methodology, each respirometer was sampled twice every hour over a continuous 24-h period. A continuous flow analyser (Alpkem RFA/2; Alpkem Corporation, Oregon, U.S.A.) was used to measure NH_4-N, and NO_x-N. The autoanalyser subsampled effluent water from an in-line oxygen electrode and channelled it to parallel photospectrometers via peristaltic pumps. Reagents (see below) were mixed with the inflowing sample and a pressurized flow of nitrogen gas from a cylinder was used to separate the flow of mixture into discrete bubbles in the peristaltic flow. The respective reactions produced colour changes, which were measured in spectrophotometric cells. Oxygen consumption was measured using an oxygen electrode (WTW TriOXmatic 601, Retsch, the Netherlands) with the data logged by the computer and on a chart recorder. Ammonia N was measured using a variation of the phenol–hypochlorite method. A unit of sample was mixed with an equal amount of lubricating solution of soap (Brij-35) and a complexing reagent (150 mL of 71 $g \cdot L^{-1}$ sodium hydrogen phosphate and 120 mL of 75 $g \cdot L^{-1}$ sodium salicylate ($2\text{-}(OH)C_6H_4CO_2Na$) mixed with 0.15 $g \cdot L^{-1}$ sodium nitroferropentacyanide ($Na_2Fe(CN)_5NO \cdot 2H_2O$); 75 mL of 10 M sodium hydroxide; 3.6 mL of 30% (v/v) Brij-35; made up to 600 mL. Equal volumes of phenol and sodium hypochlorite (5.25%, v/v) were then mixed with the sample–complex mix. The mixture then passed through a mixing coil heated to 50°C for 2 min before passing into the photometer, which read the absorbence of the solution at 640 nm; these data were recorded automatically on a chart recorder and computer.

Nitrate was reduced quantitatively to nitrite using a cadmium catalyst. The total nitrite was then determined as an azo dye, following diazotization with sulphanilamide and binding to a diamine. A unit of sample was mixed with a lubricating and imidazole buffer solution (600 mL of 6.8 $g \cdot L^{-1}$ imidazole ($C_3H_4N_2$); 1.2 mL of 0.01 M copper sulphate; 1.2 mL of Brij-35 (30%, v/v); plus 600 mL double-distilled water). The buffer–sample mix was then passed through the cadmium catalyst coil. Equal volumes of sulphanilamide (10 $g \cdot L^{-1}$ sulphanilamide ($H_2NC_6H_4SO_2NH_2$) in 10% (v/v) HCl) and diamine (1 $g \cdot L^{-1}$ 1-*N*-naphtylethylenediamine

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($C_{10}H_7NHCH_2CH_2NH_2{\cdot}2HCl$)) were added and mixed in turn. The final reaction mixture was then passed into the photospectrometer and read at 540 nm; these data were again recorded automatically.

Standard solutions of ammonia and nitrate–nitrite were made containing 0.05–1.7 $mg{\cdot}L^{-1}$ NH_3-N, 0.05–0.25 $mg{\cdot}L^{-1}$ NO_2-N, and 0.25–2.75 $mg{\cdot}L^{-1}$ NO_3-N in deionized water and used to calibrate the autosampler before and after a period of respirometry. Heinsbroek et al. (1991) reported 100% recovery of nitrogen for a series of experiments using this equipment and known quantities of standards added to the respirometers over a 24-h period. Urea excretion was measured at 0, 12, and 24 h following the meal, using the monoxime based photospectrometric method of Rahmatullah and Boyde (1980).

Dry matter of the fish (five pooled individuals from each respirometer), faeces, and food was determined by drying known amounts of sample at 105°C for 4 h to a constant weight. The lipid content of the fish body samples was determined in a Soxhlett apparatus via hexane extraction for 3 h. Ash content of the fish, faeces, and food samples was determined in a muffle furnace at 550°C.

To aid in the account of the nitrogen and energy budgets, the total nitrogen and energy contents of the effluent water was measured. At approximately 0, 8, and 20 h after feeding, duplicate 2.0 L samples of effluent water were collected from each respirometer as well as from the inflowing source. The water samples were acidified using 5 mL of 2 mol H_2SO_4 and stored (>4°C) in food-quality polyethylene bags until analysis (within 20 days). For the total N content of the water samples, a known volume (approximately 1 L) was evaporated (rotary evaporation, Heidolf 2000, Germany), and the residue was redissolved and washed out in 25 mL of H_2SO_4 before Kjeldahl digestion. To measure the energy content of the water sample, a known volume (approximately 1 L) was frozen in a food quality bag then freeze-dried. The residue was washed into a small sample bag of known mass and energetic content with 25.0 mL of double-distilled water and freeze-dried. The dry sample and bag were then combusted in a ballistic bomb calorimeter to determine the energy content of the water sample.

The efficiency with which the nitrogen and energy of the diet was apparently absorbed was calculated from the proportion of the acid insoluble ash (AIA) in the diet and the faeces with respect to the nitrogen or energy content of the diet and faeces:

$$A = 100 - [100[(AIA_d/AIA_f)(X_f/X_d)]]$$

where A is the absorption efficiency; AIA_d and AIA_f are the acid-insoluble ash in the diet and faeces, respectively; and X_d and X_f are the nitrogen or energy content in the diet and faeces, respectively. The absorption efficiencies of nitrogen and energy are calculated for each respirometer group from the mean values of the eight occasions of measurement (see Table 3).

Energy balance

The energy content of the food, faeces, fish tissue, and total energy content of the water was calculated from ballistic bomb calorimetry (Gallenkamp CBB-330-010L) in triplicate for each sample, with a typical CV ((SD/mean) × 100; %) of 0.6%. Faecal samples were conducted in duplicate. The energy content was determined by calibration with sucrose standards. Calculation of the energy balance was as described by Brafield (1985).

Oxycalorific coefficients (Q_{ox}) 13.36, 13.72, and 14.76 $J{\cdot}mg^{-1}$ oxygen for the protein, lipid, and carbohydrate components (assuming they were respired in the same proportion as absorbed) were used to calculate the amount of energy lost due to respiration from the consumption of oxygen (Carter and Brafield 1991). Relative utilization of available energy (metabolizable energy (ME); $J{\cdot}g^{-1}{\cdot}day^{-1}$) as that allocated to respiration (heat loss), total energy retention (TE; $J{\cdot}g^{-1}{\cdot}day^{-1}$), and protein energy (PE; $J{\cdot}g^{-1}{\cdot}day^{-1}$) was calculated for each of the five respirometers (see Fig. 3A).

Nitrogen balance

To establish a balance account of the N budget of the eels, the N content was measured in the source (food N) and accounted in the sinks (fish tissue; dissolved N, i.e., urea–ammonia–NO_x; faecal loss). Nitrogen contents were estimated using Kjeldahl technique. The content of pooled freeze-dried tissue, faeces, and food, as well as water samples, were analysed via automated acid digestion ($CuSO_4$–K_2SO_4 catalyst) (Tector Digestion System 20, and 1015 Lift Digester) for 90 min at 400°C and Kjeldahl analysis (Tector Analyser, Kjeltec autosampler 1035, with an Autostep 1012 controller (Kjeltec, UK)). Kjeldahl analysis of tissue samples was conducted in triplicate with a typical CV of 1.7%. Faecal N was examined in duplicate samples. Calculation of the nitrogen budget was as described by Brafield (1985).

The ammonia quotient (AQ) describes the proportion of the protein used for respiration and was defined as AQ = ammonia excreted (mol)/oxygen consumed (mol) (after Kutty 1972). AQ was calculated for each of the eight respirometry periods from the total daily ammonia excretion (sum of the hourly rates) and oxygen consumption (sum of the hourly rates). The overall mean of these eight determinations is given in Table 2, with the quotient given as AQ (mol NH_3/mol O_2).

Statistical analysis

Values are given as mean ± SD throughout. Analysis of variance (ANOVA) was used to compare means, and significant differences at the 5% level were further analysed using Tukey multiple comparison to identify means which were significantly different from one another using "Statistix" (Analytical Software, California, U.S.A.). Linear regression was by the method of least squares.

Results

Food analysis resulted in 22.8 ± 0.25 $kJ{\cdot}g^{-1}$ energy, 73.3 ± 0.32 $g{\cdot}kg^{-1}$ N, 241.1 $g{\cdot}kg^{-1}$ lipid, and 2.5 ± 0.18 $g{\cdot}kg^{-1}$ AIA content. When fed to the groups, four of the five respirometers all showed an increase in mass over the 70-day experimental period. One of the low-ration groups (low 4) had a small decrease in mass over the experimental period and thus was recorded as a negative growth rate. Another low-ration group (low 3) had a small increase in mass and so had a small specific growth rate, whilst the remaining low-ration group (low 1) showed a greater increase in mass and hence a higher rate of growth. The final mass, overall feed intake, specific growth rate (Ricker 1979), and feed conversion efficiency of each group are given in Table 1.

Ammonia excretion and oxygen consumption

The automated analysis of the rate of ammonia excretion and oxygen consumption allowed the observation of a diurnal pattern. The metabolic rate Mo_2 measured by the rate of oxygen consumption ($\mu mol\ O_2{\cdot}g^{-1}{\cdot}h^{-1}$) of each of the respirometry groups showed a rapid increase in consumption (3.00–5.50 $\mu mol\ O_2{\cdot}g^{-1}{\cdot}h^{-1}$) at approximately 12:00 (feeding time). The consumption rate of the high-ration groups remained elevated for the 12 h following the meal before declining to the diurnal low at approximately 07:00. The small peak at 08:00 coincided with an observed increase in activity at dawn. The low-ration groups had overall, a lower rate of oxygen consumption than those of high ration, although the general pattern was similar. The postprandial increase

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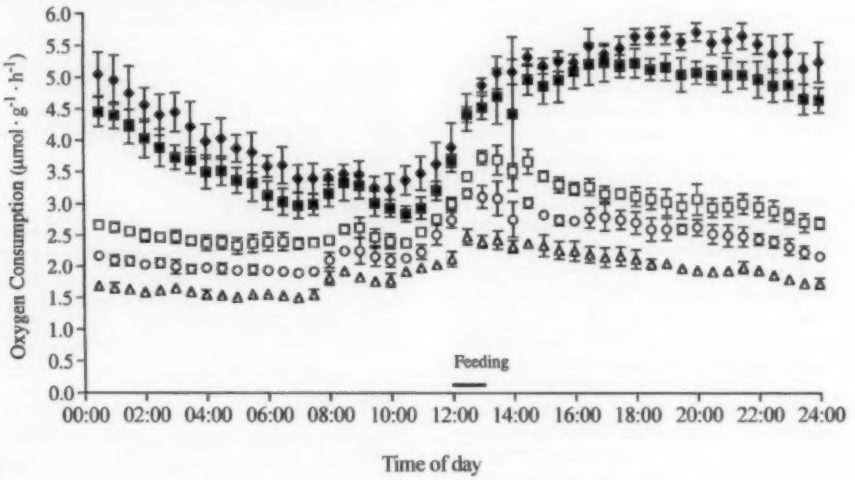
Table 1. Numbers of fish; group mass and feed intake (g wet weight); specific growth rate (%·day^{-1}) ((ln W_t – ln $W_{t=0}$) × 100/t), where t is the number of days; and gross feed conversion efficiency (feed intake/wet weight gain) in each of the respirometers.

Tank	No. of fish	Starting mass (g)	Final mass (g)	Feed intake (g)	Specific growth rate (%·day^{-1})	Gross feed conversion efficiency
Low 1	44	1917.2	2160.7	675.1	0.17	2.77
High 2	42	1763.5	3313.8	2264.8	0.90	1.46
Low 3	38	1855.9	1858.7	636.0	0.002	—*
Low 4	37	1729.1	1721.2	600.1	–0.007	—*
High 5	42	1873.8	3694.7	2419.3	0.97	1.33

*Conversion efficiency was not applicable because of near zero growth.

Fig. 1. Oxygen consumption (μmol O_2·g^{-1}·h^{-1}) of eel fed at high ration (solid diamond and square) and at low ration (open square, circle, and triangle) over a 24-h period. Values are mean ± SD (n = 8).



(2.50–3.5 μmol O_2·g^{-1}·h^{-1}) at 12:00 was a response to the feeding activity, and the slow return to the lower value over the following 10–12 h was a result of the digestion and processing of the meal (Fig. 1).

The rate of ammonia excretion (μmol N·g^{-1}·h^{-1}) over the eight periods of measurement (Fig. 2) was of a similar diurnal pattern to the oxygen consumption (Fig. 1). The two groups at high ration level showed similar patterns of greater rates of excretion than the low-ration groups. The rate of ammonia excretion of the high-ration groups started at a diurnal low at approximately 07:00 and showed a small peak at 08:00 (dawn) before returning to the diurnal low of about 0.01 μmol N·g^{-1}·h^{-1}. The rate of ammonia excretion began to increase at 10:00, two hours before feeding and before the rate of oxygen consumption began to increase. This preprandial increase in the high-ration groups resulted in more than a 10-fold increase (from about 0.01 to 0.15 μmol N·g^{-1}·h^{-1}) in the rate of ammonia excretion prior to feeding. The rate of ammonia excretion continued to increase for the 5 h following the start of feeding until reaching 0.2–0.3 μmol N·g^{-1}·h^{-1} at about 17:00. The rate of excretion then declined over the following 11 h until reaching the diurnal low of approximately 0.01–0.02 μmol N·g^{-1}·h^{-1}. The low ration groups showed a similar trend as the high ration groups; however, the postprandial increase was smaller (reaching only 0.05 μmol N·g^{-1}·h^{-1}) before it returned to the diurnal low within approximately 7 h as opposed to 11 h at high ration.

Ammonia quotient

The AQ methodology assumes that the samples (n = 8) are representative of daily oxygen consumption and ammonia excretion. The long experimental period should reduce anomalies introduced by feeding of a meal and diurnal variation. The mean (± SD) oxygen consumption and ammonia excretion (μmol·g^{-1}·day^{-1}) calculated from the eight periods of measurement are given in Table 2. From these data, the AQ (mol NH_3/mol O_2) was calculated for each respirometer. Low-ration groups, which had very low (and negative) growth rates (low 3 and 4), had significantly higher AQ (P < 0.05, n = 8) than the high-ration groups (high 2 and 5) and the low-ration group with significant growth (low 1).

The proportion of the protein used for respiration was calculated from the mean AQ and expressed as a proportion of the theoretical AQ for 100% protein respiration (Gnaiger and Bitterlich 1984). Therefore, the maximum ratio for AQ was calculated as 1.14 mol NH_3/4.6 mol O_2 = 0.248. Growing fish were found to respire 54.4–57.7% of the available dietary protein. Those groups with very little, or negative, growth apparently respired more than 100% of the

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Fig. 2. Ammonia excretion (μmol $NH_4 \cdot g^{-1} \cdot h^{-1}$) of eel fed at high ration (solid diamond and square) and at low ration (open square, circle, and triangle) over a 24-h period. Values are mean ± SD (n = 8).

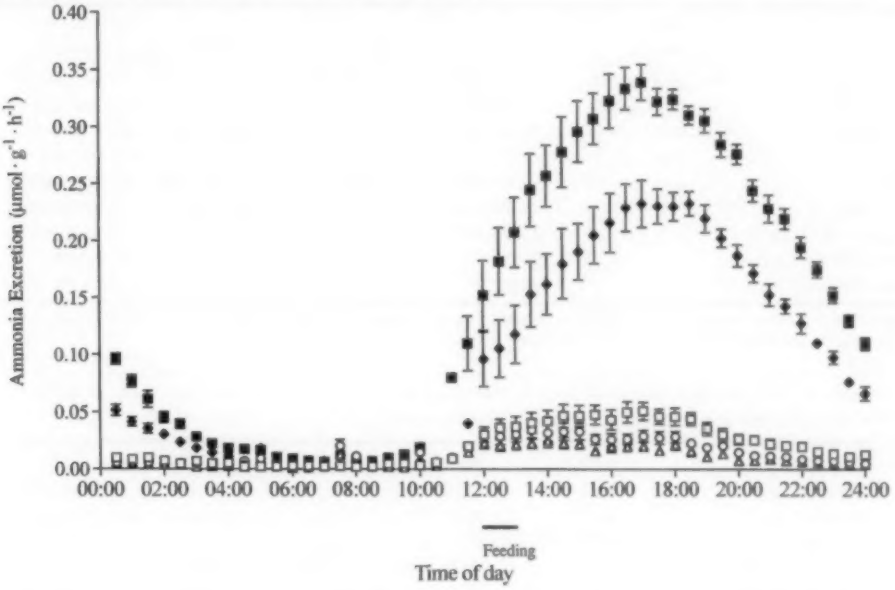

Table 2. Daily (mean ± SD, n = 8) oxygen consumption (μmol $O_2 \cdot g^{-1} \cdot day^{-1}$), ammonia nitrogen excretion (μmol NH_3-$N \cdot g^{-1} \cdot day^{-1}$), and ammonia quotient (AQ) of the groups of eels in each of the five respirometers.

Respirometer group	Low 1	High 2	Low 3	Low 4	High 5
Oxygen consumption (μmol $O_2 \cdot g^{-1} \cdot day^{-1}$)	67.82±1.34	110.86±0.93	57.11±2.49	45.53±3.11	100.47±1.04
Ammonia excretion (μmol $NH_3 \cdot g^{-1} \cdot day^{-1}$)	10.04±1.02	14.93±1.33	15.33±0.91	15.08±0.83	14.37±1.87
AQ (mol NH_3/mol O_2)	0.148±0.002*a*	0.135±0.001*a*	0.268±0.002*b*	0.331±0.003*b*	0.143±0.002*a*
% Protein respired*	59.7	54.4	108.1	133.5	57.7

Note: Values followed by the same letter are not significantly different from one another at the 5% level.

*Percent protein respired was based on a maximum AQ (100% of protein respired) of 0.248 calculated from the theoretical oxidation of an average protein containing 4.42 mol carbon, 7.00 mol hydrogen, 1.44 mol oxygen, and 1.14 mol nitrogen, which when respired aerobically would consume 4.6 mol O_2 and yield 1.14 mol NH_3.

available dietary protein. The low-ration group that underwent growth (low 1) was found to respire 59.7% of the absorbed protein (Table 2).

Absorption efficiency and body and faecal composition

The content of the body and faeces (g·kg wet weight^{-1}), nitrogen (g N·kg dry matter^{-1}), energy (kJ·g dry matter^{-1}), and lipid (g·kg dry matter^{-1}) determined by Kjeldahl, bomb calorimetry, and Soxhlett for initial samples and from each respirometer are given in Table 3. Absorption efficiency of nitrogen and energy was calculated from the mean feed and faecal contents and the mean AIA of the feed and faeces and values are given for each respirometry group in Table 3.

Nitrogen budget

The overall N budget for each of the respirometers was calculated for the 70-day period for each of the components of the budget (g N). The proportion of each channel was calculated as a percentage of the absorbed N (consumption) (Table 4). The overall balance accountability, expressed as the sum of the measured channels calculated as a percentage of the consumption, indicated that the experiment successfully accounted for most of the N. The growing groups had an accountability of 98.2, 99.0, and 101.2% and the low, and negative, growth groups had a lower accountability of 94.1 and 89.6% (Table 4).

The groups fed at a high ration level (high 2 and 5) showed similar allocation of the available N within the budget. The rate of faecal N loss was very similar at 8.4 and 8.3% of the consumed nitrogen. The proportion of the N retained as protein growth was 57.1 and 59.7% of that consumed. The loss of N to overall excretion was similar for each group at 33.5 and 32.9% of the consumption, the major proportion of which was ammonia excretion (29.8 and 29.1% of consumption), with urea representing a small proportion of the overall nitrogenous excretion (2.6 and 2.7% of consumption). Nitrate and nitrite accounted for 1.1% of the measured nitrogenous excretion.

The groups fed at a low ration level showed a more divergent distribution of the N allocation. This may be a reflection of the differing allocation of N to excretion and growth. The fish of low 1 had greater growth (0.17%·day^{-1}) than the other two (low 3 and 4) low-ration groups, (0.002 and –0.007%·day^{-1}, respectively). Group low 1 nitrogen distribu-

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Table 3. Body composition, apparent absorption efficiency, and faecal composition of eels from an initial sample and from each of the five respirometer groups after 70 days.

	Initial sample	Low 1	High 2	Low 3	Low 4	High 5
Body nitrogen (g N·kg^{-1})	59.87±1.47	54.73±0.05	55.94±1.47	57.28±0.76	59.21±0.57	53.25±0.98
Body energy (kJ·g DM^{-1})	30.90±0.95	30.93±0.24	31.30±0.25	30.31±0.31	30.42±0.04	31.71±0.13
Body lipid (g·kg DM^{-1})	542.3	581.5	590.6	535.7	558.1	549.3
Dry matter (g·kg^{-1})	388.9	422.2	411.0	397.0	387.8	420.6
Faecal energy (kJ·g^{-1})	—	12.40±0.35	13.92±0.63	12.15±0.54	12.14±0.50	13.53±0.47
Faecal nitrogen (g N·kg^{-1})	—	46.48±1.53	48.57±2.62	46.73±2.57	47.28±1.20	48.09±2.36
Faecal acid insoluble ash (g·kg^{-1})	—	25.40±1.81	19.61±2.29	25.74±2.01	24.52±2.34	19.67±2.87
Nitrogen absorption efficiency (%)	—	93.76	91.55	93.81	93.42	91.66
Energy absorption efficiency (%)	—	94.65	92.22	94.83	94.58	92.46

Note: Body composition values are means ± SD of triplicate samples. Faecal composition values are the means ± SD of pooled daily faeces from the eight periods of respirometry determined in triplicate. DM, Dry mass.

Table 4. Total nitrogen budget of each respirometer over the 70 days of the experiment in grams of nitrogen and as a percentage of 100% consumption.

Respirometer	Low 1	High 2	Low 3	Low 4	High 5
Consumption (g N)	46.39	151.97	43.73	41.09	162.53
Retention (g N)	13.32	86.72	0.16	–0.47	96.96
(% consumed)	28.7	57.1	0.4	–1.1	59.7
Excretion (g NH_3-N)	24.33	45.20	33.63	30.96	47.31
(% consumed)	52.4	29.8	76.9	75.3	29.1
Excretion (g NO_x-N)	1.47	1.71	1.57	1.32	1.93
(% consumed)	3.2	1.1	3.3	3.2	1.1
Excretion (g urea N)	3.52	3.91	3.09	2.31	4.76
(% consumed)	7.5	2.6	6.6	5.6	2.7
Faecal loss (g N)	2.90	12.84	2.71	2.70	13.56
(% consumed)	6.3	8.4	6.2	6.6	8.3
Balance (g N)	45.54	150.38	41.16	36.82	164.52
(% consumed)	98.2	99.0	94.1	89.6	101.2

tion allocated 6.3% to faecal loss, 28.7% to protein retention, and 63.1% to nitrogenous excretion, of which 52.4% of the consumed N was excreted as ammonia, 7.5% as urea and 3.2% as nitrate and nitrite. The low, and negative, growth groups (low 3 and 4) had similar distribution of the available N. Faecal loss accounted for 6.2 and 6.6%, respectively, of the consumed N. Protein retention accounted for 0.4 and –1.1%, respectively, of the consumption. Nitrogenous excretion of these two groups represented the greatest proportion of the consumed N (86.8 and 84.1%, respectively). Ammonia excretion was the greatest single channel of the N budget of these two groups, accounting for 76.9 and 75.3%, respectively, of the consumed N. Urea represented 6.6 and 5.6%, respectively, of the budget, and nitrate and nitrite were 3.3 and 3.2%, respectively, of the consumed N, respectively.

Energy budget

The overall energy budget for each of the respirometers was calculated for the 70-day period for each of the components of the budget (kJ). The proportion of each channel was calculated as a percentage of the absorbed energy (consumption) (Table 5). The overall balance accountability, expressed as the sum of the measured channels calculated as a percentage of the consumption, indicated that the experiment accounted for a large proportion of the energy in respirometers 1, 2, and 5 but less successfully in respirometers 3 and 4. The growing groups had an accountability of 92.3, 86.5, and 88.6% and the low, and negative, growth groups had a lower accountability of 65.2 and 53.4% (Table 5).

The groups fed at a high ration level (high 2 and 5) showed similar allocation of the available energy within the budget. The rate of faecal energy loss was very similar at 7.8 and 7.5%, respectively, of the consumed energy. The proportion of the energy retained as growth was 41.8 and 47.6%, respectively, of that consumed. The loss of energy to overall excretion was similar and represented a small proportion for each group at 2.6% of the metabolizable energy. A large proportion of the metabolizable energy was allocated to respiration (heat loss) with 34.2 and 30.9%, respectively, used.

As in the N budget, groups fed at a low ration level showed a more divergent distribution of the energy allocation than the high-ration groups. This may be a reflection of the cost of respiration, which represented a larger proportion of the metabolizable energy at low ration levels. Group low 1 used the greatest proportion of the metabolizable energy, 60.2%, in respiration (heat loss). Respiration accounted for 53.0 and 42.1% of the energy budget in the low-growth groups (low 3 and 4, resrpectively), which was less than in group low 1 but higher than in the high-growth groups. Group low 1 lost 5.3% of the consumed energy to faecal

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Table 5. Total energy budget (kJ) of each respirometer over the 70-day period and the proportion of the budget as a percentage of the absorbed (consumed) energy.

Respirometer	Low 1	High 2	Low 3	Low 4	High 5
Consumption (kJ)	14 580	47 656	13 761	12 950	51 039
Retention (kJ)	3 179	19 943	34	–93	24 285
(% consumed)	21.8	41.8	0.3	–0.7	47.6
Excretion (kJ) (NH_3+NO_x)	641	1 166	875	802	1 224
(% consumed)	4.4	2.4	6.4	6.2	2.4
Excretion (kJ) (urea N)	80	87	70	52	108
(% consumed)	0.5	0.2	0.5	0.4	0.2
Heat loss (kJ)	8 781	16 320	7 287	5 453	15 773
(% consumed)	60.2	34.2	53.0	42.1	30.9
Faecal loss (kJ)	780	3 706	712	703	3 847
(% consumed)	5.3	7.8	5.2	5.4	7.5
Balance (kJ)	13 461	41 222	8 978	6 917	45 237
(% consumed)	92.3	86.5	65.2	53.4	88.6

loss, which was very similar to the faecal losses of groups low 3 and 4. Energy retention as growth in group low 1 accounted for 21.8% of the consumed energy, whilst in groups low 3 and 4, this portion of the energy budget was apparently missing because of little (and negative) growth, which would have accounted for 0.3 and –0.7% of the consumed energy. The missing portion of the energy balance may also have been attributable to the relatively small changes in body composition, which may well increase the proportion of apparently missing energy. Group low 4 underwent a weight loss over the experimental period. Since the overall balance (ignoring the contribution from the tissue catabolism) of this group was less accurate than the growing groups (53.4%) then the contribution produced via the derivation of this energy may well have been high. The proportion of the energy budget lost to nitrogenous excretion was small, in group low 1 (4.9%) and a little higher in groups low 3 and 4 (6.9 and 6.6%).

Deposition of metabolizable energy

The proportion of the metabolizable energy (ME; $J \cdot g^{-1} \cdot day^{-1}$) deposited as total energy retention (TE; $J \cdot g^{-1} \cdot day^{-1}$) and protein energy (PE; $J \cdot g^{-1} \cdot day^{-1}$) at the different energy intakes are described by the linear regressions of Fig. 3A. The difference between ME and TE was that proportion of the energy intake utilized by respiration (heat loss). The relationship of TE to ME indicated that 83.8 $J \cdot g^{-1} \cdot day^{-1}$ (63.7/0.76) are required to maintain energy equilibrium. The difference between total energy retention and protein energy retention represented the nonprotein substrate retention, for example, lipid, carbohydrate, and bone growth. From the relationships described by Fig. 3A, the proportion of the energy that would be expected to be deposited in protein was $(0.45/0.76) \times 100 = 59.2\%$.

Deposition of available protein

The proportion of the available N (AN; mg $N \cdot g^{-1} \cdot day^{-1}$) deposited as protein (PN; mg $N \cdot g^{-1} \cdot day^{-1}$) and excreted as metabolic waste (EN; mg $N \cdot g^{-1} \cdot day^{-1}$) at the two feeding levels is described by Fig. 3B. Regression analysis of the proportion of the N excreted at the two rations was significant, as was the proportion of the available N incorporated into protein. The PN in excess of EN is that retained as protein growth. The intercept of the PN line would indicate that 0.28 mg $N \cdot g^{-1} \cdot day^{-1}$ was necessary to satisfy maintenance requirements.

Discussion

Growth

The specific rate of growth over the experimental period shown by the high-ration groups (0.90 and 0.97%·day^{-1}) is approaching the freshwater growth rate of 1.2%·day^{-1} found on commercial farms (Knights 1985). The body composition of the eels sampled before and after the experimental period were similar (Table 3); therefore, growth is a realistic reflection of the energy deposition by the animals and justifies the use of the standard energy constants (Jobling 1993). The very low (and negative) rates of growth of two of the low-ration groups appear to indicate a close approximation of the maintenance ration for the eel. However, one of the low ration groups (low 1) showed a growth rate of 0.17%·day^{-1}, which indicated that the ration level was in excess of maintenance. The reason for this difference in growth rates between groups of eels fed at the same rate is unclear and may be due to any of a number of factors, such as differences in activity in the groups or social hierarchy effects on the feeding efficiency (Owen 1996).

Nitrogen excretion and oxygen consumption

The rate and pattern of ammonia excretion of the eels in this investigation is similar to previous investigations (Heinsbroek et al. 1991) of the eel in the same apparatus and at similar rations. The daily rate of ammonia excretion is of the same order as that found by Agradi et al. (1995). Urea excretion of the eels measured in this study represented 8.7 ± 2.0% of the total nitrogenous excretion, which is less than the 30–50% estimated by Heinsbroek et al. (1991) but in line with 6–12% measured by Agradi et al. (1995).

The rate of oxygen consumption is marginally higher than that measured by Heinsbroek et al. (1991). The postprandial increase in metabolic rate of fish is known as the apparent specific dynamic action (ASDA) and is most likely associated with the synthesis of proteins (Carter and Brafield 1991) and feeding metabolism (Jobling 1983).

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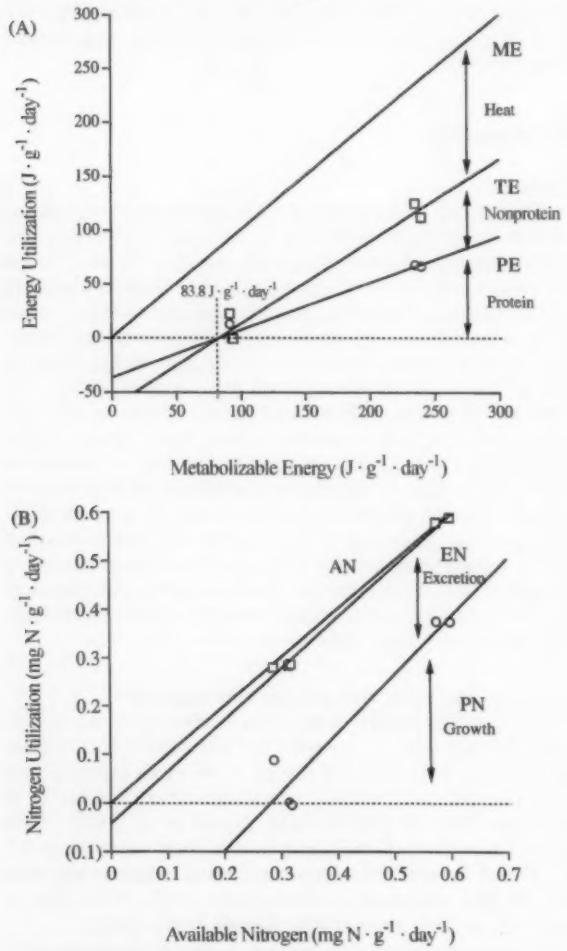
Fig. 3. (A) Model of energy utilization described by energy budgets of the eels fed high and low rations. Metabolizable energy (ME) is the energy available for metabolism (J·g fish^{-1}·day^{-1}), and is partitioned between heat loss and growth. Total energy (TE) is the total energy retained as growth, and protein energy (PE) is the energy retained as protein. The model describes the utilization of total energy as TE = 0.76ME – 63.7 (n = 5, r = 0.98, P < 0.01) and PE = 0.45ME – 36.4 (n = 5, r = 0.99, P < 0.01). (B) Model of the nitrogen utilization described by the nitrogen budgets of the eels fed at high and low ration levels. Available nitrogen (AN) is the nitrogen absorbed from the meal (mg N·g fish^{-1}·day^{-1}) and is partitioned between growth and excretion. Excretory nitrogen (EN) is the total nitrogen excreted (ammonia, NO_x, and urea), and protein nitrogen (PN) is the nitrogen retained as growth. The model describes the utilization of the excretory nitrogen as EN = 1.1 AN – 0.04 (n = 5, r = 0.997, P < 0.001) and nitrogen retention (growth) as PN = 1.2 AN – 0.34 (n = 5, r = 0.96, P < 0.01).



The proportion of the protein used in respiration in the high-ration groups (54.4 and 57.7%) is within the range of the 45–85% found previously for eel (Heinsbroek et al. 1991). The low-ration fish were unable to spare protein for retention as growth since metabolism accounted for more than 100% of the protein available from food. This implies that body protein was respired, as was the body lipid (Table 3).

Errors in the measurement of excretion and oxygen consumption at the low-ration treatment may have been larger than at high ration because of the dilution of the smaller quantities involved and therefore were more likely to be less accurately determined because of the sensitivity of the methods. This may contribute to the apparently large imbalance in the energy budget of the low-ration fish, in addition to the effect of changes in body composition.

Energy and nitrogen balances

The methods used to determine the N balance of each respirometry group can be considered to be valid, since close to 100% accountability was found. The measurement of each individual channel of the budget has its own margin of error, which must be considered when judging the accuracy of the balance (Brafield 1985; Carter and Brafield 1991). All measures were made repeatedly on eight separate occasions, 1 week apart. This long period of time should reduce the effect of single measurement errors and the error associated with the rate of growth in short-term studies. The balance was constructed over the 70-day period using mean values from each of the eight occasions of respirometry. Respirometry over a 24-h period in flow-through conditions minimized the flush-out time effect described by Steffensen (1989), since the integral of the consumption or excretion rate is calculated for the complete diurnal cycle. The rate of consumption was determined as the total food consumption over the period (measured daily to the nearest 0.1 g). Nitrogen retention was calculated from the nitrogen content of the representative body samples from each group and the change in wet weight. The representative body tissue samples were from animals that had the same nutritional and environmental histories, so as to provide samples which were as representative as possible. Composition determinations have their own error, although this was kept to a minimum via replicate samples (Table 3). Faecal losses other than those determined, such as through leaching, are considered to be very small because of the design of flow-through system and short contact time with the water. These faecal losses include N loss in the form of a mucal coating enveloping the faeces, and some gall fluid (as described by Heinsbroek et al. (1991)). Since the balance was close to 100% (and nitrogen content of water samples was not significantly different to that accounted for by ammonia, nitrate–nitrite, and urea), nitrogenous loss in the form of shedding mucus and sloughing cells may account for a small proportion of the imbalance in addition to the measurement errors.

The energy balance for each respirometer was apparently less accurate than the N balance. The accuracy of the determinations used in the nitrogen balance are equally valid for the energy determinations. However, the additional channel of respiration costs (heat loss) may well be an underestimate of the actual costs since the Q_{ox} values are based upon the assumption that the substrates are utilized in the same proportions as they are absorbed (Brafield 1985). Errors in this assumption are likely to be small (Carter and Brafield 1991); however, combined with costs of swimming and any repair

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of damage due to aggression, an underestimate of the respiratory heat loss may account for a proportion of the incomplete budget.

Energy budget

The generalized energy budgets of carnivorous and herbivorous fish constructed by Brett and Groves (1979) are such that it appears that the major difference between the two styles of feeding is in the efficiency of absorption. Herbivorous fish are apparently less efficient at extracting the energy from the meal and loose more of the available energy to the faecal component of the budget. Since the generalized balances for the eels of this study are incomplete, comparisons must be made with caution. However, losses of energy through poor absorption are of similar proportions at high and low rations, although the absolute losses are larger at high ration levels (Table 5). The relatively small proportion of the energy budget allocated to faecal loss in eels when compared with the general model of Brett and Groves (1979) may be due to the use of the highly digestible diet specifically designed for eel aquaculture, since an underestimate due to leaching from the faeces is unlikely because of the experimental conditions used. The proportion of energy lost through nitrogenous excretion is similar for each ration level, although nitrogenous excretion may well account for a larger proportion of the budget at lower rations. The major differences between high and low ration sizes is apparently in the proportion of the energy balance allocated to respiratory heat loss and retained production. At high ration levels, the absolute amount of respiratory loss is higher than low rations, but the proportion of the total balance is considerably smaller. This provides a large proportion of the available energy to be retained as production. The absolute amount of energy used in respiration at a low ration is less than at high ration (Table 5). However, this represents a large proportion of the available energy.

Cui and Wootton (1988*a*) suggest that comparisons between species should only be made at maximum rations. The high ration level of this experiment approaches the maximum ration of the eel (Heinsbroek et al. 1991). The high-ration energy retention (41.8 and 47.6% of consumption) of these eel are similar to rainbow trout (*Oncorhynchus mykiss*; Cho and Kaushik 1985) and more than the 9.6–27.2% for growing herbivorous grass carp (*Ctenopharyngodon idella*; Carter and Brafield 1991) and the 21–35% for the six species feeding at maximum ration listed by Cui and Liu (1990*a*). This is in accordance of the general balances of Brett and Groves (1979).

Koch and Wieser (1983) found that the roach (*Rutilus rutilus*) reduced its swimming activity during gonadal development, significantly reducing the energy costs of locomotion. The energy spent in locomotion (swimming) is included in the respiratory loss proportion of the budget. The costs of swimming were not measured for the eels, and it was assumed that the costs would be the same for each group since they were housed and treated identically. If feeding behaviour is taken into account, then the costs of swimming may account for a proportion of the unaccounted balance of the energy budgets, and the differences in these unaccounted losses between the high and low rations. A study of the feeding behaviour of individual eels kept in groups fed at high and low ration levels was conducted concurrently with this experiment (Owen 1996). The principle result of that investigation was that there was a higher degree of variation in the mean share of a group meal for individuals fed at a low ration level than at high ration. This could be attributed to the increased competition in feeding at low rations, because of the reduced availability of food. If this theory is pursued, then the increased competition at low rations may result in a higher degree of activity than at high rations. This would result in a larger amount of energy spent in competing for less food. Swimming is generally regarded as being of relatively low cost for fish, but as Koch and Wieser (1983) have shown, this can use significant amounts of energy. Anguilliformes swim in a different manner to the roach, which generally uses only the last third of the body for normal swimming (Jobling 1985). Eels, however, use a larger proportion of the body for swimming, which is a result of waves of motion down the length of the body (Gillis 1997). Although this study provides no evidence in the form of high oxygen consumption, it is intuitive that the anguilliform style of swimming may require more energy than say a roach.

Eels are carnivorous, and there have been several investigations into their aggressive behaviour (e.g., Knights 1987). If the restriction of the available food increases the overall degree of aggression, then the activity of the eels will increase. The difference in activity between high- and low-ration groups may provide a proportion of the unaccounted budget.

Nitrogen budget

The overall N budgets show a close approximation to a complete balance (Table 4). Since all channels of the N budget were estimated independently of one another, the close approximation to 100% accountability for each group would tend to support a general accuracy within the methodology. The interindividual variation in protein content, and the use of representative pooled samples to estimate protein growth (N retention) is likely to introduce the greatest margin of error. Previous studies have successfully attempted to reduce the effect of this inherent problem by calculating N retention by difference, i.e., consumed N minus faecal and nitrogenous excretion (Carter and Brafield 1992). However, in the present study, estimation of nitrogen retention by difference appears unnecessary since the balance is close to 100% (Jobling 1993).

The rate of nitrogen excretion is affected by several biotic and abiotic factors, such as ration size and quality, body size, and temperature (Brafield 1985; Cui and Wootton 1988*a*, 1998*b*, 1988*c*; Cui and Liu 1990*a*, 1990*b*; Carter and Brafield 1992). Ammonia generally represents the largest proportion of the total nitrogenous excretion in freshwater teleosts (Randall and Wright 1987), with urea contributing a smaller proportion. Neither high nor low ration level feeding, in this study, changed the excretory pattern. Although the weight-specific rate of nitrogenous excretion (ammonia) is greater at high than low ration levels (Fig. 2), the proportion of the consumed N allocated to ammonia excretion was higher in the low ration groups 78 ± 13% than at the high ration groups 33.5 and 32.9%. Urea represented a small, con-

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Table 6. The standard metabolic rate of 14 species of fish measured (or calculated) at similar temperatures.

Species	Body weight (g)	Temperature (°C)	Standard metabolic rate ($J \cdot g^{-1} \cdot day^{-1}$)	Reference
Cyprinid, *Pseudorasbora parva*	0.86–2.14	25	63.4	Cui and Liu 1990*b*
Anabantid, *Macropodus chinensis*	0.86–2.14	25	75.8	Cui and Liu 1990*b*
Goldfish, *Carassius auratus*	0.86–2.14	25	77.1	Cui and Liu 1990*b*
Carp, *Cyprinus carpio*	0.86–2.14	25	85.9	Cui and Liu 1990*b*
Bagarid catfish, *Pseudobagarus fulvidraco*	0.86–2.14	25	98.5	Cui and Liu 1990*b*
Tilapia, *Oreochromis mossambicus*	0.86–2.14	25	111.8	Cui and Liu 1990*b*
Southern catfish, *Silurus meridionalis*	9	25	120	Xie and Sun 1993
	128	25	72	
Grass carp, *Ctenopharyngodon idella*	63	22	119.3[a]	Carter and Brafield 1991
	55	22	117.3[b]	
	74	22	46.9[c]	
Eel, *Anguilla anguilla*	75	25	83.3	This study
White sturgeon, *Acipenser transmontanus*	5	18.5	309	Cui et al. 1996
Grass carp, *Ctenopharyngodon idella*	12	30	432	Cui et al. 1994
Values calculated by Cui and Liu 1990*b*				
Threespine stickleback, *Gasterosteus aculeatus*	1	25	183	
Minnow, *Phoxinus phoxinus*	1	25	223	
Alewife, *Alosa pseudoharengus*	1	25	244	
Lake trout, *Salvelinus namaycush*	1	25	275	

stant, proportion of the total N excretion at both low 8.7 ± 2.8% and high ration 7.8 and 8.2%.

General models of energy and N utilization

The general model of energy utilization (Fig. 3A) predicts a larger proportion of the available ME to be retained as protein growth (59.2%) than was calculated from the energy budget (Table 5) (41.8–47.6% at the high ration). This difference may be due to a combination of an underestimate of the energy content of the protein (which would also aid in explaining the unaccounted portion of the energy budget) and the effect of the margin of error in the calculation of the regression coefficients of the model.

The model of the N utilization (Fig. 3B) is able to predict the amount of AN necessary for maintenance as 0.28 mg $N \cdot g^{-1} \cdot day^{-1}$. However, the EN does appear to indicate that a relatively constant percentage of the AN is allocated to excretion, although these data are inconclusive.

Respiration rate

The rate of respiration in terms of the oxygen consumption Mo_2 ($\mu mol \cdot g^{-1} \cdot h^{-1}$) given for the fish of each group in Fig. 1 fall in the range (1.5–5.5 $\mu mol \cdot g^{-1} \cdot h^{-1}$) for metabolic rates given for starving 120-g eel (1.2 $\mu mol\ O_2 \cdot g^{-1} \cdot h^{-1}$) at 21°C (Sebert et al. 1995) and feeding (4% body weight) 150-g eel at 24°C (5.8 $\mu mol\ O_2 \cdot g^{-1} \cdot h^{-1}$) (Degani et al. 1989). Recently, Cruz-Neto and Steffensen (1997) reported the equivalent of 3.8 $\mu mol\ O_2 \cdot g^{-1} \cdot h^{-1}$ for 120-g eels at 25°C, reaffirming that the standard metabolic rate of eels is similar to other teleosts and not exceptionally low as commonly believed.

Metabolizable energy

The rate of standard metabolism (defined by Cui and Liu (1990*d*) as $J \cdot g^{-1} \cdot day^{-1}$) of the eels at 25°C was 83.3 $J \cdot g^{-1} \cdot day^{-1}$ (Fig. 3A), which is within the range for a variety of species measured at similar temperatures (Table 6). Table 6 is an attempt to compare the rate of standard metabolism in a variety of herbivorous, omnivorous, and carnivorous species. However, caution must be exercised in making such comparisons from the literature. The effect of scaling must be considered by taking into account the body size of the subject animals, which were used in the original determination. The herbivorous cyprinids and anabantid have similar rates of standard metabolism to the eel. However, the eel is considered to be carnivorous and, like the bagarid, has an apparently lower standard metabolic rate than the omnivorous tilapia (*Oreochromis mossambicus*) and a considerably lower rate than the carnivorous rainbow trout, minnow (*Phoxinus phoxinus*), threespine stickleback (*Gasterosteus aculeatus*), and alewife (*Alosa pseudoharengus*). However, these rates were calculated by Cui and Liu (1990*b*) for the species at 25°C, which is likely to be at least in the upper thermal limit for all of these fish; this may explain the very high energy requirement. It is not conclusive that this apparent difference between the form of heterotrophy and the rate of standard metabolism is valid or significant. However, it does provide an interesting insight into the metabolism of fish and puts the eel with its rate of standard metabolism in a position more akin to the omnivores than the carnivores; this suggests that perceived lifestyle of an animal does not necessarily determine the metabolic rate (Secor and Diamond 1997).

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References

Adams, S.M., and Breck, J.E. 1990. Bioenergetics. *In* Methods for fish biology. *Edited by* C.B. Schreck and P.B. Moyle. American Fisheries Society, Bethesda, Md. pp. 389–415.

Agradi, E., Bonomi, L., Rigamonti, E., Liguori, M., and Bronzi, P. 1995. The effect of dietary lipid on tissue lipids and ammonia excretion in European eel, *Anguilla anguilla*. Comp. Biochem. Physiol. A, **111**(3): 445–451.

Brafield, A.E. 1985. Laboratory studies of energy budgets. *In* Fish energetics: new perspectives. *Edited by* P. Tytler and P. Calow. Croom Helm, London. pp.257–282.

Brett, J.T. 1979. Environmental factors and growth. *In* Fish physiology. Vol. VIII. Bioenergetics and growth. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, London. pp. 599–675.

Brett, J.T., and Groves, T.D.D. 1979. Physiological energetics. *In* Fish physiology. Vol. VIII. Bioenergetics and growth. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, London. pp. 279–352.

Carter, C.G., and Brafield, A.E. 1991. The bioenergetics of grass carp, *Ctenopharyngodon idella* (Val.): energy allocation at different planes of nutrition. J. Fish Biol. **39**: 873–887.

Carter, C.G., and Brafield, A.E. 1992. The bioenergetics of grass carp, *Ctenopharyngodon idella* (Val.): the influence of body weight, ration, and dietary composition on nitrogenous excretion. J. Fish Biol. **41**: 533–543.

Cho, C.Y., and Kaushik, S.J. 1985. Effects of protein intake on metabolisable and net energy values of fish diets. *In* Nutrition and feeding in fish. *Edited by* C.B. Cowey, A.M. Mackie, and J.G. Bell. Academic Press, London. pp. 95–118.

Cruz-Neto, A.P., and Steffensen, J.F. 1997. The effects of acute hypoxia and hypercapnia on oxygen consumption of the freshwater European eel. J. Fish Biol. **50**: 759–796.

Cui, Y., and Liu, J. 1990*a*. Comparison of energy budget among six teleosts—I. Food consumption, faecal production and nitrogenous excretion. Comp. Biochem. Physiol. A Physiol. **97**(1): 163–168.

Cui, Y., and Liu, J. 1990*b*. Comparison of energy budget among six teleosts—II. Metabolic rates. Comp. Biochem. Physiol. A Physiol. **97**: 169–174.

Cui, Y., and Liu, J. 1990*c*. Comparison of energy budget among six teleosts—III. Growth rate and energy budget. Comp. Biochem. Physiol. A Physiol. **97**: 381–84.

Cui, Y., and Liu, J. 1990*d*. Comparison of energy budget among six teleosts—IV. Individual differences in growth and energy budget. Comp. Biochem. Physiol. A Physiol. **97**: 551–554.

Cui, Y., and Wootton, R.J. 1988*a*. Bioenergetics of growth of a cyprinid, *Phoxinus phoxinus*: the effect of ration, temperature and body size on food consumption and nitrogenous excretion. J. Fish Biol. **33**: 431–443.

Cui, Y., and Wootton, R.J. 1988*b*. Pattern of energy allocation in the minnow, *Phoxinus phoxinus*. Funct. Ecol. **2**: 57–62.

Cui, Y., and Wootton, R.J. 1988*c*. The metabolic rate of the minnow, *Phoxinus phoxinus*, in relation to ration, body size and temperature. Funct. Ecol. **2**: 157–161.

Cui, Y. Chen, S., and Wang, S. 1994. Effect of ration size on the growth and energy budget of the grass carp, *Ctenopharyngodon idella* Val. Aquaculture, **123**: 95–107.

Cui, Y. Hung, S.S.O., and Zhu, X. 1996. Effect of ration and body size on the energy budget of juvenile white sturgeon. J. Fish Biol. **49**: 863–876.

Degani, G., Gallagher, M.L., and Meltzer, A. 1989. The influence of body size and temperature on oxygen consumption of the European eel, *Anguilla anguilla*. J. Fish Biol. **34**: 19–24.

Gillis, G.B. 1997. Anguilliform locomotion in an elongate salamander (*Siren intermedia*): effects of speed on axial undulatory movements. J. Exp. Biol. **200**: 767–784.

Gnaiger, E., and Bitterlich, G. 1984. Proximate biochemical composition and caloric content calculated from elemental CHN analysis: a stoichiometric concept. Oecologia, **62**: 289–298.

Heinsbroek, L.T.N., van Thoor, R.M.H., and Elizondo, L.J. 1991. The effect of feeding level on the apparent digestabilities of nutrients and energy of a reference diet for the European eel, *Anguilla anguilla* L., and the African catfish, (*Clarias gariepinus* Burchell). *In* Proceedings of the 3rd International Symposium on Feeding and Nutrition in Fish. Aquaculture Special Publication A. pp. 175–188.

Jobling, M. 1983. Towards an explanation of specific dynamic action (SDA). J. Fish Biol. **23**: 549–555.

Jobling, M. 1985. Growth. *In* Fish energetics: new perspectives. *Edited by* P. Tytler and P. Calow. Croom Helm, London. pp. 213–230.

Jobling, M. 1993. Bioenergetics: feed intake and energy partitioning. *In* Fish ecophysiology. *Edited by* J.C. Rankin and F.B. Jensen. Chapman & Hall, London. pp. 1–44.

Knights, B. 1985. Energetics and fish farming. *In* Fish energetics: new perspectives. *Edited by* P. Tytler and P. Calow. Croom Helm, London. pp. 309–340.

Knights, B. 1987. Agonistic behaviour and growth in the European eel, *Anguilla anguilla* L., in relation to warm-water aquaculture. J. Fish Biol. **31**: 265–276.

Koch, F., and Wieser, W. 1983. Partitioning of energy in fish: can reduction of swimming activity compensate for the cost of production? J. Exp. Biol. **107**: 141–146.

Kutty, M.N. 1972. Respiratory quotient and ammonia excretion in *Tilapia mossambica*. Mar. Biol. **16**: 126–133.

Owen, S.F. 1996. Protein turnover determined using a stable isotope [^{15}N], feeding behaviour and bioenergetics in fish. Ph.D. thesis, University of Dundee, Dundee, Scotland.

Rahmatullah, M., and Boyde, T.R.C. 1980. Improvements in the determination of urea using diacetyl monoxime, methods with and without deproteinisation. Clin. Chim. Acta, **107**: 3–9.

Randall, D.J., and Wright, P.A. 1987. Ammonia distribution in fish. Fish Physiol. Biochem. **3**: 107–120.

Ricker, W.E. 1979. Growth rates and models. *In* Fish physiology. Vol. VIII. Bioenergetics and growth. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, London. pp. 677–743.

Sebert, P., Pequeux, A., Simon, B., and Barthelemy, L. 1995. Effects of hydrostatic pressure and temperature on the energy metabolism of the Chinese crab (*Eriocheir sinensis*) and the yellow eel (*Anguilla anguilla*). Comp. Biochem. Physiol. A Physiol. **112**(1): 131–136.

Secor, S., and Diamond, J. 1997. Determinants of the postfeeding metabolic response Burmese pythons, *Python molurus*. Physiol. Zool. **70**(2): 202–212.

Steffensen, J.F. 1989. Some errors in respirometry of aquatic breathers: how to avoid and correct for them. Fish Physiol. Biochem. **6**: 49–59.

Van Waarde, A. 1983. Aerobic and anaerobic ammonia production by fish. Comp. Biochem. Physiol. B Biochem. Mol. Biol. **74**: 675–684.

Xie, X.J., and Sun, R. 1993. Pattern of energy allocation in the southern catfish (*Silurus meridionalis*). J. Fish Biol. **42**: 197–207.

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Effects of growth and fatness on sexual development of chinook salmon (*Oncorhynchus tshawytscha*) parr

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Abstract: The independent effects of size and fatness, 1 year prior to maturity, on male sexual development of chinook salmon (*Oncorhynchus tshawytscha*) were tested. Beginning in March 1995, ration size and dietary lipid were independently manipulated to produce four groups of spring chinook salmon differing in size and fatness. Size, growth rate, adiposity, liver triacylglycerol and glycogen contents, and plasma insulin and insulin-like growth factor I (IGF-I) levels were monitored to follow the metabolic states of fish in the different treatment groups and to observe whether plasma levels of these growth mediators predict sexual development. Differences in size and fatness were well established by the first autumn (September 1995), 1 year prior to sexual maturity, and common ration size groups were pooled for further rearing. Subsequently in winter–spring (February–March), 6 months prior to sexual maturity, there were no within-tank differences in size or fatness. Nevertheless, the effects of size and fatness, from 1 year earlier, on incidence of sexual maturity were significant. Overall, size appeared to have the primary effect, but for smaller fish, an effect of fat content was indicated. Plasma insulin levels, and in limited cases, IGF-I levels, were correlated with growth rate and size, but were not accurate indicators of sexual development.

Résumé : Les auteurs ont testé les effets indépendants de la taille et de l'adiposité, 1 an avant l'atteinte de la maturité, sur le développement sexuel de quinnats (*Oncorhynchus tshawytscha*) mâles. À partir du mois de mars 1995, on a manipulé indépendamment la ration et les lipides alimentaires de manière à obtenir quatre groupes de quinnats de printemps différant par la taille et l'adiposité. On a surveillé la taille, le taux de croissance, l'adiposité, la concentration de triacylglycérol et de glycogène dans le foie et la teneur du plasma en insuline et en facteur de croissance insulinoïde I (IGF-I), afin de suivre l'état métabolique des poissons des différents groupes et de déterminer si les concentrations plasmatiques des médiateurs de croissance examinés permettent de prévoir le développement sexuel. Des différences de taille et d'adiposité étaient manifestes dès le premier automne (septembre 1995), 1 an avant que les poissons atteignent la maturité sexuelle, et les groupes recevant la même ration ont été groupés pour la poursuite de l'élevage. Par la suite, en hiver et au printemps (février–mars), 6 mois avant d'atteindre la maturité sexuelle, les poissons des différents bassins ne présentaient aucune différence de taille ou d'adiposité. Néanmoins, les effets de la taille et de l'adiposité de l'année précédente sur l'incidence de la maturité sexuelle étaient importants. En général, il semble que l'effet principal soit dû à la taille, mais dans le cas des poissons de petite taille, on a attribué un certain effet à l'adiposité. Les concentrations d'insuline plasmatique, et dans un petit nombre de cas, d'IGF-I, étaient corrélées au taux de croissance et à la taille, mais elles n'étaient pas des indicateurs précis du développement sexuel.

[Traduit par la Rédaction]

Introduction

The great intra- and inter-population variation in age at sexual maturity exemplifies the tremendous plasticity in life history patterns of salmonid fishes. This plasticity results in fish reaching maturity from 1 to 7 years of age. While age at sexual maturity has been shown to be influenced by both genetic and environmental factors (Rowe and Thorpe 1990; Silverstein and Hershberger 1992), the physiological mechanisms by which maturity is triggered are not clear. There is considerable evidence that large size, fast growth rate, and high lipid content are important criteria for initiation of sexual development (Rowe et al. 1991; Silverstein and Shimma 1994; Silverstein et al. 1997). The complex relationship be-

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tween diet composition, feeding rate, growth, and energy storage has made it difficult to isolate the effects of any single factor on maturation. Furthermore, underlying these complex interactions is a circannual cycle (Gorbman et al. 1982; Foote et al. 1992).

Sexual maturation and the parr–smolt transformation are major life history transitions for salmon. Both these events are the culmination of developmental processes that must be initiated months earlier (Scott and Sumpter 1983; Thorpe 1986; Plisetskaya et al. 1988). The periods at which such developmental processes are entrained have been called "critical periods" or "windows" (Policansky 1983).

Two critical periods have been hypothesized to occur along the pathway leading to gonadal development and sexual maturity for salmon (Mangel 1994; Berglund 1995). One is in autumn (September–November) about 1 year before sexual maturation, and the second is in spring (March–May) about 6 months prior to maturity. These critical periods for sexual development and maturation are proposed to be set by environmental cues (e.g., photoperiod) near the autumnal and vernal equinoxes (Scott and Sumpter 1983; Thorpe 1991). At these critical periods, individuals "evaluate" their developmental potential in terms of growth rate, size, or stored energy or some combination of these factors and either continue along the developmental pathway leading to maturity or suspend development and wait another year to mature. The simplest conceptualization of the "evaluation" is probably a threshold model, where surpassing a given value for size, growth rate, or energy storage will trigger the developmental steps toward sexual maturity (cf. Roff 1996). The two critical periods for maturation mentioned above are proposed to differ. In the second period (6 months prior to maturation), gonadal development already in progress can either continue to advance or be turned off (Rowe and Thorpe 1990; Berglund 1995), but an individual not developing since the first critical period (the previous autumn) cannot initiate gonadal development (Mangel 1994).

Both size and fatness have been strongly implicated as threshold characters with minimum values that must be surpassed for maturation to ensue (Saunders et al. 1982; Rowe et al. 1991; Silverstein et al. 1997). However, the typically high correlation between size and fatness has made independent appraisal of these two factors difficult (Shearer 1994; Shearer et al. 1997).

Our study was designed to examine two facets of the critical period/threshold model for maturation in chinook salmon (*Oncorhynchus tshawytscha*). First, we wanted to test the independent effects of size and fatness on sexual maturity. Second, we aimed to test the hypothesis that fish condition 1 year prior to sexual maturity affected maturation rates. By manipulating ration size and dietary protein to lipid ratio, we developed a procedure to permit independent control of growth and energy storage in chinook salmon (Shearer et al. 1997). Using this paradigm, we were able to compare the main effects of ration size and dietary lipid and their interaction on growth, energy storage, and sexual development. In addition to measuring growth, body fat, and liver glycogen and triacylglycerol storage in the experimental groups, the growth mediators insulin and insulin-like growth factor I (IGF-I) were evaluated to examine the endocrine response to differences in ration size and dietary energy and to determine the anabolic state of the animals. We determined whether the status of the fish during the autumn 1 year prior to sexual maturity influenced the incidence of sexual maturity by producing groups with large differences in size and body fatness by September 1995 and then combining size groups and exposing fish to a similar environment.

Our specific objectives were to (*i*) examine the independent effects of growth (ration level) and fatness (dietary lipid) on the incidence of male sexual maturity, (*ii*) establish the endocrine profiles of insulin and IGF-I in fish receiving different ration size and dietary protein to lipid ratios, and (*iii*) determine if fish condition in autumn, 1 year prior to sexual maturity, influences the rate of sexual maturity.

Material and methods

Animals

Spring chinook derived from the 1994 broodyear (BY 1994) population of the Willamette River Hatchery in Oregon were used. Embryos were obtained in November 1994 and incubated at the Northwest Fisheries Science Center, Seattle, Wash. Rearing conditions were described previously by Shearer et al. (1997). Briefly, at first feeding (January 1995), alevins were fed a commercial starter feed (BioDiet-starter, Bioproducts, Warrenton, Oreg.). When the fish reached a mean weight of 0.66 g, they were counted into lots of 400 and placed into eight 700-L tanks supplied with flow-through dechlorinated municipal water at 6 L/min. Over the course of the first phase of this experiment, the dietary treatment phase (January–September 1995) water temperatures ranged from 6 to 17°C, reflecting the natural temperature cycle, except for 4 days in September 1995 when temperatures reached 20°C due to a failure of the refrigeration unit. During the second phase of the experiment (October 1995 – June 1996), fish were maintained on a recirculating water system at a constant 12°C under an ambient photoperiod.

Diets and feeding regime

The diet preparation procedures and feeding regime used during the dietary treatment phase of this experiment have been described previously (Shearer et al. 1997). To summarize, diets were prepared monthly at the appropriate pellet size and frozen at –20°C until being fed. In order to vary dietary lipid, two diets were prepared by adding different amounts of lipid to a basal mix so that one diet contained 85% protein and 3% lipid (low lipid, LL) and the other contained 65% protein and 23% lipid (high lipid, HL). A high-protein cod muscle meal was used as the protein source and herring oil was the lipid source.

Food was fed at two levels: high ration (HR) and low ration (LR). The amount of food fed to the HR group was determined by feeding all HR groups to apparent satiation and recording the amount of food consumed on day 1 of the dietary treatment. For the rest of the first month, all HR groups received 90% of the amount of food consumed by the HR group eating the least on day 1. Fish were fed slightly below satiation to insure that all feed would be consumed. LR groups were fed half this amount. When mortalities occurred, the dead fish were weighed and the ration reduced by the approximate weight of food consumed by those fish, predicted by the fraction of the total tank biomass represented by the dead fish. The ration amounts were calculated each month in a similar manner on the day following monthly tissue and weight sampling. The amount of food fed to each tank was adjusted for the preceding month's feed efficiency (weight gain/dry feed fed) and number of fish in each tank in order to keep fish within a ration group closely matched for size. Further details of this iterative feeding regime are given in Shearer et al. (1997).

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Table 1. Weights (g, mean ± SE) of treatment groups during the 1995 dietary treatment phase of the experiment.

Date	HR/HL	HR/LL	LR/HL	LR/LL
Jan. 20	0.7	0.7	0.7	0.7
Mar. 1	1.6±0.03*a*	1.5±0.04*a*	1.3±0.03*b*	1.3±0.02*b*
Mar. 29	2.5±0.02*a*	2.6±0.10*a*	1.9±0.04*b*	1.9±0.03*b*
Apr. 26	3.9±0.2*a*	3.9±0.2*a*	2.6±0.2*b*	2.5±0.2*b*
May 24	5.0±0.3*a*	5.0±0.3*a*	3.1±0.2*b*	3.1±0.2*b*
June 22	8.2±0.6*a*	9.3±0.4*a*	3.9±0.3*b*	4.0±0.2*b*
July 19	11.4±1.0*a*	11.5±0.6*a*	5.6±0.4*b*	4.7±0.3*b*
Aug. 23	14.2±1.5*a*	14.4±1.0*a*	5.9±0.4*b*	6.6±0.3*b*
Sept. 28	20.8±2.5*a*	20.3±1.6*a*	8.7±0.7*b*	7.5±0.6*b*

Note: Values within a row (sampling day) followed by different letters are significantly different. Data for January 20, March 1, and March 29 are means of bulk-weighed tanks (n = 2); data for April 26 – September 28 are means of 30 fish (15 individuals per tank, two tanks per treatment).

Table 2. Whole-body fat levels (%, mean ± SE) in treatment groups during the 1995 dietary treatment phase of the experiment.

Date	HR/HL	HR/LL	LR/HL	LR/LL
Jan. 20	3.89	3.89	3.89	3.89
Mar. 1	5.12±0.15*a*	2.69±0.04*b*	4.59±0.11*a*	2.19±0.07*b*
Mar. 29	6.75±0.34*a*	3.41±0.08*bc*	5.07±0.27*ab*	2.63±0.23*c*
Apr. 26	8.96±0.12*a*	5.72±0.66*bc*	6.52±0.04*ab*	3.30±0.11*c*
May 24	7.16±0.49*a*	3.22±0.05*bc*	5.58±0.38*ab*	2.28±0.08*c*
June 22	7.98±0.15*a*	4.16±0.40*b*	4.71±0.28*b*	2.90±0.13*b*
July 19	10.78±0.15*a*	5.84±0.52*bc*	6.80±0.35*b*	3.82±0.24*c*
Aug. 23	8.69±0.01*a*	4.81±0.57*b*	5.47±0.21*b*	3.30±0.21*b*
Sept. 28	11.25±0.11*a*	5.40±0.07*c*	7.08±0.01*b*	3.89±0.01*d*

Note: Values within a row (sampling day) followed by different letters are significantly different. Whole-body fat values are the means of replicate tanks (n = 2); each tank mean was calculated from 10 individuals.

With these two dietary manipulations, ration size and dietary lipid, four treatment groups were produced: high ration/high lipid (HR/HL), high ration/low lipid (HR/LL), low ration/high lipid (LR/HL), and low ration/low lipid (LR/LL). All treatments were applied to duplicate groups of fish between March 1995 and September 1995.

In October 1995, after the feeding treatments had been applied for 7.5 months, the second phase of the experiment was begun. The purpose of this phase of the experiment was to examine the effect of autumn differences in size and fatness on sexual maturity 1 year later. Therefore, in order to reduce environmental variations as much as possible during subsequent rearing, HR fish from both HL and LL groups were differentially marked by pelvic fin clips and combined. LR fish were similarly marked and combined for a further 7.5 months of rearing. After combining these groups, replicates were no longer identifiable. During this second phase of the experiment, fish were fed to satiation once daily with a commercially available salmon feed (BioDiet) containing 44.5% protein and 14.5% lipid. In June 1996, the experiment was terminated and all fish dissected to evaluate sexual maturity.

Sampling

Beginning in March 1995 when fish were 3 months posthatch, monthly sampling was conducted through September 1995 to collect data on weight (nearest 0.1 g). Ten fish per group were sampled for lipid content analyses, and an additional 5–10 individuals per group were sampled for plasma and liver samples. Food was withheld for 1 day prior to sampling, and all sampled fish were anesthetized with MS 222. After combining treatment groups by ration level for rearing to sexual maturity, weight, body fat, and plasma samples were collected in February–March and June 1996. During the final sampling in June, gonads were weighed and evaluated macroscopically. A clear bimodality in testes size was evident and the males with larger testes were considered to be sexually maturing. A post hoc comparison of the gonadosomatic index (GSI) (gonad weight (grams) × 100/total weight (grams)) between fish judged to be maturing and immature was made.

Analyses

Specific growth rate during sampling intervals was calculated as $\ln (W_2) - \ln (W_1) \times 100/d$, where W_2 is the mean weight (grams) at the end of the interval, W_1 is the mean weight (grams) at the beginning of the interval, and d is the number of days within the interval.

For lipid content analyses, fish were weighed, minced, and dried to constant weight at 105°C. Dried fish were ground with a mortar and pestle and lipid was then extracted from a 1-g sample using a Soxhlet device with 100 mL of dichloromethane as the solvent. The solvent was refluxed for 2 h. Lipid content is reported on a wet weight basis.

Blood was collected with heparinized syringes or heparinized capillary tubes for measurement of plasma levels of insulin and IGF-I. Samples for plasma insulin and IGF-I were stored at –80°C for later analysis following the protocols of Plisetskaya (1994) and Moriyama et al. (1994), respectively.

Livers were removed from the fish, frozen immediately on dry ice, and stored at –80°C until glycogen and triacylglycerol content analysis by the methods of Plisetskaya et al. (1994) (glycogen) and Silverstein et al. (1997) (triacylglycerol).

Statistical analyses

Ration size and dietary lipid effects were first examined by two-way analysis of variance (ANOVA). Subsequently, replicate within-treatment effects were tested and when not significant, all fish within a treatment were pooled and treatment effects were tested by one-way ANOVA followed by Tukey–Kramer multiple comparison procedures. To examine treatment effects on incidence of maturity after replicate tanks had been pooled, a three-dimensional chi-square test of independence was conducted (number mature, ration size, dietary fat) followed by two-way tests of partial independence (Zar 1984). Correlation analyses were also carried out using within-sample individual values and across-sample treatment mean values. The associations between insulin and IGF-I plasma levels with growth rate were investigated by simple correlation analysis of the treatment mean hormone levels versus the treatment mean growth rate for the period ending with the hormone sample (i.e., May insulin level versus April–May growth rate). Significance for all analyses was established at the $P < 0.05$ level.

Results

Mortality over the dietary treatment phase of the experiment was 7%. Most fish died either during the first month of feeding or in September 1995 when the water refrigeration unit failed. There was no difference in mortality among treatments. Mortality in the second phase of the experiment was 4%, due mainly to a brief malfunction in the dechlorination system.

The fish reared under these feeding regimes varied in both size and body lipid (Tables 1 and 2). Weight and body lipid

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Fig. 1. (*a*) Mean liver triacylglycerol content from May to September 1995 and (*b*) mean liver glycogen content from April to September 1995 in the treatment groups. Different letters indicate significant difference within months. Open circles, HR/HL; solid circles, HR/LL; open squares, LR/HL; solid squares, LR/LL.

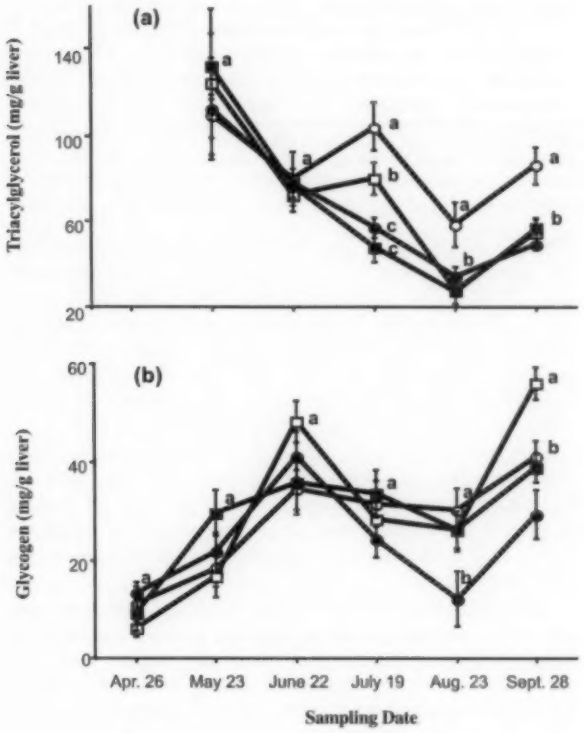
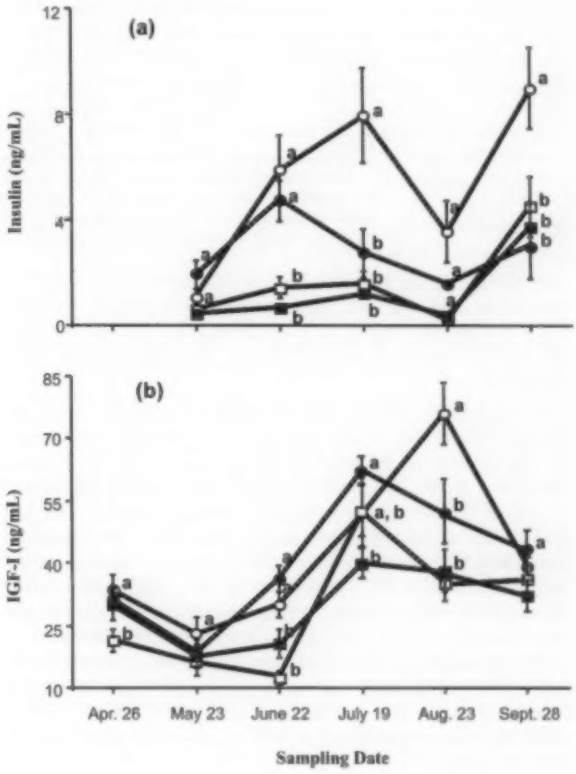


Fig. 2. (*a*) Mean plasma insulin from May to September 1995 and (*b*) mean plasma IGF-I from April to September 1995 in the treatment groups. Different letters indicate significant difference within months. Open circles, HR/HL; solid circles, HR/LL; open squares, LR/HL; solid squares, LR/LL.



differences between replicates were not significant, and therefore, all replicate data were pooled. Treatment differences in size and body fat were apparent by the first sample after beginning the treatments (March 1) (Tables 1 and 2). By September 1995, we had produced four groups of fish that were paired for size, yet had large differences in body fat (see also Shearer et al. 1997).

The specific growth rate patterns were similar among groups, declining after a high in the January–March interval. Due to small sample sizes, differences in specific growth rate between groups were generally not significant; however, growth rates diverged in May–June as the HR groups grew rapidly. Thereafter, growth rates converged.

Liver samples were analyzed for triacylglycerol and glycogen content. Liver triacylglycerol content of the HR/HL fish was significantly greater than in the other groups from July to September; however, differences in whole-body fat between groups had a clearer separation than liver triacylglycerol (Fig. 1*a*). Whole-body fat content increased between May and September, while liver triacylglycerol content per gram of liver declined. A seasonal pattern in liver glycogen content was observed (Fig. 1*b*), peaking in June and declining to its lowest point in August, but no consistent pattern of variation developed between groups.

Plasma insulin values showed both seasonal variations across treatments and differences based on treatment (Fig. 2*a*). A general increase in insulin levels was seen between May and July across groups coincident with increasing body fat contents, and the correlation between insulin levels and body fat from May to September 1995 was highly significant ($r = 0.77$, $P < 0.001$). Nevertheless, there were significant differences by ration size in that HR groups had higher insulin levels at each month with the exception of September.

IGF-I plasma levels also showed a seasonal trend (Fig. 2*b*), rising from June to July and remaining stable with a small decline in values through September. IGF-I levels correlated significantly with body fat ($r = 0.46$, $P = 0.04$), although not as strongly as insulin. Like insulin, IGF-I levels between groups differed most consistently with ration level, with HR groups having higher IGF-I levels, although in September, neither ration nor dietary fat level had a significant effect on IGF-I levels. In plasma samples collected in February 1996, 5 months after pooling treatment groups, there

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Table 3. Weights (g, mean ± SE) and fat contents (% lipid, mean ± SE) of the treatment groups in September 1995 at the end of the dietary treatment and in the spring before maturity (March 1996 (weight) and February 1996 (% lipid)) and % maturity in June 1996.

	Weight		% lipid		% maturity
Treatment	Sept. 1995 (n = 30)	Mar. 1996 (n = 20)	Sept. 1995 (n = 2)	Feb. 1996 (n = 5)	(June 1996) (n)
HR/HL	20.8±2.5*a*	42.5±7.5*ab*	11.3±0.2*a*	8.1±0.6*a*	36.4 (44)*a*
HR/LL	20.3±1.6*a*	53.3±6.6*a*	5.4±0.1*c*	7.8±0.5*a*	31.6 (57)*a*
LR/HL	8.7±0.7*b*	32.5±4.2*b*	7.1±0.0*b*	5.3±0.5*b*	21.3 (47)*b*
LR/LL	7.5±0.6*b*	28.0±2.4*b*	3.9±0.0*d*	5.6±0.8*b*	7.0 (57)*c*

Note: Values within a column followed by different letters are significantly different. % maturity is the number of mature males/number of males. Values for % lipid in September are the treatment means based on measurement of 10 individuals from each of two replicates; those for February are the treatment means based on five individuals from each treatment.

was no difference between any of the treatment groups for insulin or IGF-I levels. Mean values in February (insulin, 3.8 ± 0.4 ng/mL; IGF-I, 37.4 ± 3.9 ng/mL) were in the middle of the range observed during April–September 1995 sampling.

In June 1996, during final sampling to evaluate sexual development, insulin levels did not vary between treatments, but the difference between maturing (3.9 ± 0.4 ng/mL) and immature males (1.7 ± 0.2 ng/mL) was highly significant ($P < 0.001$). Plasma from females was not sampled. In addition to the association with maturation state, insulin levels correlated with weight, both within samples (insulin versus weight correlation for June: $r = 0.62$, $P < 0.001$) and across all samples (mean insulin versus mean weight correlation from March 1995 to June 1996: $r = 0.64$, $P < 0.003$).

The associations between the growth mediators insulin and IGF-I and growth rate were examined. The correlation between insulin and growth rate was $r = 0.53$, $P < 0.02$, while the correlation between IGF-I and growth rate was $r = 0.05$, $P > 0.80$.

Body weight and fat levels measured in February–March 1996 showed that there was no difference in weight or fat levels within ration groups. Nevertheless, the HR groups did maintain a size advantage over the LR groups, and the larger, HR fish were also fatter (Table 3).

Rates of maturity differed among the groups (Table 3). All maturing fish were male. Mean GSI for maturing and immature fish was 2.60 ± 0.24 and 0.03 ± 0.001, respectively. A clear separation between maturing and immature fish was seen at a GSI of 0.07; however, three fish judged to be mature, based on testicular thickening, had a GSI of <0.06. Chi-square analyses showed that ration and dietary fat level together had a significant effect on incidence of maturity (HR/HL, 36%; HR/LL, 32%; LR/HL, 21%; LR/LL, 7%; df = 3, $P < 0.002$) (see Table 3). Furthermore, ration alone had a significant effect on incidence of maturity whereas the effect of dietary fat level alone was not significant. This last test indicated that the inhibitory effect on sexual development of low levels of dietary fat during the year prior to maturity was only significant under the LR regime.

Discussion

Close correlation between size and body fat (Brett et al. 1969; Simpson 1992) has impeded attempts to distinguish the independent effects of size and fatness on sexual maturity (Rowe et al. 1991; Simpson 1992; Silverstein et al. 1997). We were able to modify size and fatness independently by controlling both ration size and dietary lipid. Additionally, differences in size and fatness, in place by September 1995, had an effect on the incidence of sexual maturity 1 year later in these spring chinook salmon.

Fish growth in weight, during the dietary treatment phase, was controlled by ration size. Because our diets were already high in protein, dietary fat did not increase the amount of protein used for growth (i.e., spare protein, cf. Takeuchi et al. 1978), and body fat accumulated in relation to the amount of fat fed.

After combining fish in October 1995, fish size had a major effect on lipid content and on sexual development. Larger fish were fatter and matured at a higher rate. This shows that ration size during the dietary treatment phase of the experiment, and not dietary fat level, determined spring body fat content. Additionally, it appears that for the larger fish on the HR diet, variation in dietary lipid 1 year earlier did not affect incidence of maturation whereas for the smaller LR fish, variation in dietary lipid and fatness 1 year earlier did appear to affect maturation rates.

In February–March 1996 when interim samples were collected, there were no significant within-tank differences in fatness or size. Therefore, later differences in sexual development had presumably stemmed from differences in lipid content or size already in place by September 1995. It is recognized, however, that to go from significantly different fat storage levels in September to a uniform level of body fatness by February, differences in energy intake and (or) utilization throughout the winter must have occurred, and these difference may also have impacted sexual development. Both LL groups exhibited large increases in lipid between September 1995 and February 1996, suggesting compensatory acquisition and storage. It has been suggested that the rate of fat storage could be an important permissive signal for maturation (Thorpe 1986).

The size of fish in the LR/HL and LR/LL treatments was not significantly different in September 1995 or in March 1996; however, at both time periods the LR/HL fish had higher mean values for weight. Because the incidence of maturity increases rapidly with size near a threshold (Simp-

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son 1992; Berglund 1995), an effect of size on maturity for the LR fish cannot be ruled out.

Because the larger, leaner HR/LL fish matured at higher frequency than the smaller, fatter LR/HL fish, we may suppose that size had the primary effect and the effect of fatness was subsidiary to size. However, we must be cautious in this interpretation. The total amount of fat (total weight × percent fat) is greater in the larger, leaner fish. The percentage of body fat in September was higher in the LR/HL fish (7.1 versus 5.4%), but the total fat content was higher in the HR/LL fish (1.1 versus 0.6 g). Further studies are needed to examine whether the effect of fat is substrate mediated depending on the total amount of fat or whether the proportion of energy stored as fat is sensed by the fish, in which case the percentage of body weight may be critical.

Plasma levels of the anabolic hormones insulin and IGF-I reflected growth through August, but did not appear to be good indicators of sexual development in the autumn 1 year prior to sexual maturity nor in spring 6–7 months prior to sexual maturity. While both hormones were associated with ration size and therefore growth rate in the dietary treatment phase, mean insulin levels were more highly correlated with mean growth rate than were IGF-I levels. Similar correlations between salmonid fish size and circulating plasma insulin have been reported previously (Mommsen and Plisetskaya 1991; Sundby et al. 1991). The absence of correlation between growth rates and IGF-I plasma levels in this study is puzzling (cf. Beckman et al. 1998). It deserves further study and may possibly depend on interactions between IGF-I and IGF-binding proteins (IGFBPs) (Gentil et al. 1996). It is known that when IGF-I is bound to IGFBPs, its activity is altered (Zapf 1997). The relatively high water temperatures the fish experienced in this study (12°C) may also have influenced the plasma levels of anabolic hormones.

In the final sample collected in June, insulin levels were associated with size and incidence of maturity (maturing fish were larger). Although in June, we found no association between IGF-I plasma levels and maturity, a significant negative effect of maturity on IGF-I plasma levels has been demonstrated in salmon closer to final maturation (Moriyama et al. 1997).

Endocrine measures of anabolic activity and growth rate differences in the summer, more than 1 year prior to sexual maturity, were successful in distinguishing ration size effects on growth, but less useful in distinguishing diet composition effects on growth.

Differences in our treatment groups were apparent as early as March 1995 and persisted to September 1995, but within ration group had disappeared by February–March 1996. This shows that fish condition in the autumn preceding sexual maturity has an effect on rates of sexual maturity 1 year later. By combining nutritional and physiological approaches, we have clarified the roles of size and fatness and demonstrated an interaction between these two factors.

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References

Beckman, B.R., Larsen, D.A., Moriyama, S., Lee-Pawlak, B., and Dickhoff, W.W. 1998. Environmental modulation of the growth hormone-insulin like growth factor I endocrine axis and its relation to size, growth and smoltification in juvenile spring chinook salmon (*Oncorhynchus tshawytscha*). Gen. Comp. Endocrinol. **109**: 325–335.

Berglund, I. 1995. Effects of size and spring growth on sexual maturation in 1+ Atlantic salmon (*Salmo salar*) male parr; interactions with smoltification. Can. J. Fish. Aquat. Sci. **52**: 2682–2694.

Brett, J.R., Shelbourn, J.E., and Shoop, C.T. 1969. Growth rate and body composition of fingerling sockeye salmon (*Oncorhynchus nerka*) in relation to temperature and ration size. J. Fish. Res. Board Can. **26**: 2363–2394.

Foote, C.J., Wood, C.C., Clarke, W.C., and Blackburn, J. 1992. Circannual cycle of seawater adaptability in *Oncorhynchus nerka*: genetic differences between sympatric sockeye salmon and kokanee. Can. J. Fish. Aquat. Sci. **49**: 99–109.

Gentil, V., Martin, P., Smal, J., and LeBail, P-Y. 1996. Production of recombinant insulin-like growth factor-II in the development of a radioimmunoassay in rainbow trout (*Oncorhynchus mykiss*). Gen. Comp. Endocrinol. **104**: 156–167.

Gorbman, A., Dickhoff, W.W., Mighell, J.L., Prentice, E.F., and Waknitz, W. 1982. Morphological indices of developmental progress in the parr–smolt coho salmon, *Oncorhynchus kisutch*. Aquaculture, **28**: 1–19.

Mangel, M. 1994. Climate change and salmonid life history variation. Deep-Sea Res. **41**: 75–106.

Mommsen, T.P., and Plisetskaya, E.M. 1991. Insulin in fishes and agnathans: History, structure and metabolic regulation. Crit. Rev. Aquat. Sci. **4**: 225–259.

Moriyama, S., Swanson, P., Nishii, M., Takahashi, A., Kawauchi, H., Dickhoff, W.W., and Plisetskaya, E.M. 1994. Development of a homologous radioimmunoassay for coho salmon insulin-like growth factor-I. Gen. Comp. Endocrinol. **96**: 149–161.

Moriyama, S., Shimma, H., Tagawa, M., and Kagawa, H. 1997. Changes in plasma insulin-like growth factor-I levels in the precociously maturing amago salmon *Oncorhynchus masou ishikawai*. Fish Physiol. Biochem. **17**: 253–259.

Plisetskaya, E.M. 1994. Development of radioimmunoassay for a model peptide hormone: insulin. *In* Biochemistry and molecular biology of fishes. *Edited by* P.W. Hochachka and T.P. Mommsen. Elsevier, Amsterdam, The Netherlands. pp. 535–542.

Plisetskaya, E.M., Swanson, P., Bernard, M., and Dickhoff, W.W. 1988. Insulin in coho salmon (*Oncorhynchus kisutch*) during the parr to smolt transformation. Aquaculture, **72**: 151–164.

Plisetskaya, E.M., Moon, T.W., Larsen, D.A., Foster, G.D., and Dickhoff, W.W. 1994. Liver glycogen, enzyme activities and pancreatic hormones in juvenile Atlantic salmon (*Salmo salar*) during their first summer in seawater Can. J. Fish. Aquat. Sci. **51**: 567–576.

Policansky, D. 1983. Size, age, and demography of metamorphosis and sexual maturation in fishes. Am. Zool. **23**: 57–63.

Roff, D.A. 1996. The evolution of threshold traits in animals. Q. Rev. Biol. **71**: 3–35.

Rowe, D.K., and Thorpe, J.E. 1990. Suppression of maturation in male Atlantic salmon (*Salmo salar* L.) parr by reduction in feeding and growth during spring months. Aquaculture, **86**: 291–313.

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Rowe, D.K., Thorpe, J.E., and Shanks, A.M. 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci.. **48**: 405–413.

Saunders, R.L., Henderson, E.B., and Glebe, B.D. 1982. Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). Aquaculture, **28**: 211–229.

Scott, A.P., and Sumpter, J.P. 1983. The control of trout reproduction: basic and applied research on hormones. *In* Control processes in fish physiology. *Edited by* J.C. Rankin, T.J. Pitcher, and R.T. Duggan. John Wiley & Sons, New York. pp. 200–220.

Shearer, K.D. 1994. Factors affecting the proximate composition of cultured fishes with emphasis on salmonids. Aquaculture, **119**: 63–88.

Shearer, K.D., Silverstein, J.T., and Dickhoff, W.W. 1997. Manipulation of growth and adiposity of juvenile chinook salmon. Aquaculture, **157**: 311–323.

Silverstein, J.T., and Hershberger, W.K. 1992. Precocious maturation in coho salmon (*Oncorhynchus kisutch*): estimation of the additive genetic variance. J. Hered. **83**: 282–286.

Silverstein, J.T., and Shimma, H. 1994. Effect of restricted feeding on early maturation in female and male amago salmon, *Oncorhynchus masou ishikawae*. J. Fish Biol. **45**: 1133–1135.

Silverstein, J.T., Shimma, H., and Ogata, H. 1997. Early maturity in amago salmon (*Oncorhynchus masu ishikawai*): an association with energy storage Can. J. Fish. Aquat. Sci. **54**: 444–451.

Simpson, A.L. 1992. Differences in body size and lipid reserves between maturing and non-maturing Atlantic salmon parr, *Salmo salar*, L. Can. J. Zool. **70**: 1737–1742.

Sundby, A., Hemre, G.I., Borreback, B., Christophersen, B., and Blom, A.K. 1991. Insulin and glucagon family peptides in relation to activities of hepatic hexokinase and other enzymes in fed and starved Atlantic salmon (*Salmo salar*) and cod (*Gadus morhua*). Comp. Biochem. Physiol. **100**: 467–470.

Takeuchi, T., Watanabe, T., and Ogino, C. 1978. Supplementary effects of lipids in a high protein diet of rainbow trout. Nippon Suisan Gakkaishi, **44**: 677–681.

Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. *In* Salmonid age at maturity. *Edited by* D.J. Meerburg. Can. Spec. Publ. Fish. Aquat. Sci. No. 89. pp. 7–14.

Thorpe, J.E. 1991. Acceleration and deceleration effects of hatchery rearing on salmonid development and their consequences for wild stocks. Aquaculture, **98**: 111–118.

Zapf, J. 1997. Total and free IGF serum levels. Eur. J. Endocrinol. **136**: 146–147.

Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, N.J.

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Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model

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Abstract: To assess extinction risk for Oregon coastal coho salmon, *Oncorhynchus kisutch*, we developed a life cycle model based on habitat quality of individual stream reaches estimated from survey data. Reach-specific smolt output was a function of spawner abundance, demographic stochasticity, genetic effects, and density- and habitat-driven survival rates. After natural mortality and ocean harvest, spawners returned to their natal reaches. Populations in reaches with poor habitat became extinct during periods of low marine survival. With favorable marine survival, high productivity reaches served as sources for recolonization of lower quality reaches through straying of spawners. Consequently, both population size and distribution expanded and contracted through time. Within a reach, populations lost resilience at low numbers when demographic risk factors became more important than density-dependent compensation. Population viability was modeled for three coastal basins having good, moderate, and poor habitat. With constant habitat conditions, extinction risk in 99 years was negligible in basins with good and moderate habitat and 5–10% in the basin with poor habitat. Reductions in habitat quality up to 60% in 99 years resulted in reduced coho salmon populations in all basins and significantly increased extinction risk in the basin with poor habitat.

Résumé : Pour évaluer le risque d'extinction du coho, *Oncorhynchus kisutch*, des eaux côtières de l'Oregon, nous avons élaboré un modèle du cycle biologique basé sur la qualité de l'habitat de divers tronçons de cours d'eau, estimée d'après des données obtenues par relevé. La production de smolts par tronçon était fonction de l'abondance des géniteurs, de la stochasticité de la démographie, des effets génétiques et des taux de survie liés à l'habitat et à la densité. Après avoir été soumis à la mortalité naturelle et aux captures en mer, les géniteurs reviennent à leur cours d'eau de naissance. Les populations des zones où l'habitat est dégradé ont disparu après des périodes de faible survie en mer. Quand la survie en mer était favorable, les zones à forte productivité ont servi de source pour la recolonisation des tronçons de faible qualité par des géniteurs égarés. C'est ainsi que l'effectif de la population et sa distribution se sont élargis et rétrécis avec le temps. Sur un même tronçon, les populations ont perdu leur résilience à faible effectif lorsque les facteurs de risque d'ordre démographique sont devenus plus importants que la compensation dépendante de la densité. Nous avons modélisé la viabilité de la population pour trois bassins côtiers présentant des habitats de qualité bonne, modérée et faible. Si les conditions de l'habitat demeuraient constantes, le risque d'extinction en 99 ans était négligeable dans les bassins où l'habitat était bon et modéré, et de 5–10% dans les bassins où l'habitat était de faible qualité. Une réduction de 60% de la qualité de l'habitat en 99 ans causait une baisse de la population de coho dans tous les bassins, et accroissait de façon notable le risque d'extinction dans le bassin où l'habitat était de faible qualité.

[Traduit par la Rédaction]

Introduction

The probability that a population will become extinct over a specified period of time has been suggested as a standard by which to classify relative vulnerability to extinction (Thompson 1991; Allendorf et al. 1997). This standard has commonly been expressed as a 5% probability of extinction (Allendorf et al. 1997; Goodman 1999) or, conversely, a 95% probability of persistence (Thompson 1991) over the next 100 years. Population viability analysis (PVA) is the structured process of assessing this vulnerability (Shaffer 1990). PVA has been applied to a variety of species, from butterflies (Murphy et al. 1990) to grizzly bears, *Ursus arctos* (Shaffer 1981). Recent concern over threats to Pacific salmon have led to analyses of chinook salmon, *Oncorhynchus tshawytscha*, in the Snake River, Idaho (Emlen 1995), the Umpqua River, Oregon (Ratner et al. 1997), and the Sacramento River, California (Botsford and Brittnacher 1998).

Coho salmon, *Oncorhynchus kisutch*, populations on the Oregon coast have been fragmented as a result of habitat destruction, with the result being relatively high densities remaining in only a few streams (Cooney and Jacobs 1995; Nickelson 1998). Murphy et al. (1990) suggested that PVA for species with fragmented habitats "must focus on the en-

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vironmental factors and metapopulation characteristics that determine local population persistence." We have developed a model that takes this approach by incorporating the contribution of fish from individual stream reaches of differing qualities. The model mimics the life cycle of coho salmon and simulates population fluctuations and random dispersal over years by incorporating density-driven compensation and depensation, short-term stochastic variation in survival, long-term climatic cycles, reduced genetic fitness from small population size, and straying of spawners from their natal spawning areas. Habitat quality determines the number of coho salmon smolts that a stream can produce as well as the efficiency with which those smolts are produced (i.e., survival rate). Production within a basin was estimated for individual stream reaches, based on habitat quality data. The result is a model that incorporates population dynamics, environmental variability, genetic factors, and metapopulation structure.

The model was used in a PVA to assess extinction probabilities of single cohorts of Oregon coastal coho salmon at the basin scale. We used three basins of varying habitat quality to represent the range of conditions on the Oregon coast. We tested the sensitivity of populations in these three basins to varying levels of marine survival and exploitation rates over 30 years (10 generations). We simulated the effects of a range of starting population sizes, including the 1995 actual spawner escapements, on median population size and probability of extinction in 99 years (33 generations). We also modeled the effects of changes in habitat quality on persistence and population size.

To estimate extinction probabilities rigorously would require incorporating "everything that is known and everything that is not known about the *dynamics* of the population" (Goodman 1999). We have not achieved this ambitious goal; therefore, our results in this area must be viewed as exploratory.

Methods

Coho salmon life cycle

We based our model on the life cycle of coho salmon in Oregon. Coho salmon in coastal streams typically spawn from early November through mid-January. Juveniles emerge from the gravel in spring and typically spend a summer and winter in freshwater (primarily in second- to fifth-order streams) before migrating to the ocean as smolts in their second spring. A very small percentage of juveniles (<5%) spend an additional winter in freshwater, migrating to the ocean in their third spring (Moring and Lantz 1975). Precocious males, called jacks, return to freshwater at the end of one summer in the ocean as age 2 spawners. They comprise about 20% of each run (Moring and Lantz 1975). Adult coho salmon return to freshwater after their second summer in the ocean as age 3 spawners. Because of the predominance of age 3 adults in Oregon coho salmon populations, they are considered to have three brood cycles.

Model

The general approach taken here was to use reach-specific production parameters derived from Nickelson's (1998) habitat limiting factors model (HLFM) to model coho salmon production in a river basin. Each reach represented a population, modeled separately through processes of egg production, egg-to-parr survival, parr-to-smolt survival, marine survival, harvest, and spawner escapement. Populations in a basin were linked through straying of spawners among reaches. Successive generations were simulated by using spawners from one generation to seed the next. Stochastic variation was included at several stages of the life cycle model. Monte Carlo simulations were used to produce a set of likely outcomes from a set of input parameters. Details of the modeling at each life stage are described below.

Spawners

Spawners were the starting point for the simulations and the ending point for each generation. For the purpose of the model, spawners included only age 3 adults, thus a 3-year generation time. For simplification, jacks were not included in the calculations. Similarly, because age 4 adults are very rare, they were also excluded from the model. The absence of these two age-classes from the modeled populations could possibly result in an underestimation of the productive potential of the modeled populations (Botsford and Brittnacher 1998) because of the lost contribution to the reproductive capacity of successive broods.

Wild coho salmon in coastal Oregon streams tend to spawn over a period of 2–3 months (Cooney and Jacobs 1995), preventing fish spawning early from interacting with fish spawning later. This usually is not a problem when populations are large; spawners should have little difficulty finding mates. However, when spawner populations are very small and some fish are present in a stream early and others late, finding a mate could become a matter of chance. A spawner not finding a mate is a depensatory effect of small spawner numbers. To simulate the effects of this depensation, time of spawning was split into three periods: early, middle, and late. Spawners in each reach were assigned randomly to the three periods. The number of female spawners in each time period was drawn from a binomial distribution where $p = 0.5$ and n is the number of spawners in the time period. There are no reliable data for the sex ratio of wild coho salmon in Oregon, and the data for hatchery coho salmon are conflicting. With 20% of males returning as jacks, it is likely that more than half of the returning age 3 adults are females. However, given the lack of consistent data, we modeled a 50:50 sex ratio.

Eggs

Egg deposition was calculated as 2500 eggs per female (Moring and Lantz 1975; Oregon Department of Fish and Wildlife (ODFW), unpublished data for 1990–1995). When marine survival was <0.8%, a fecundity reduction of 24% was applied to simulate the effects of El Niño (Johnson 1988); low marine survival, associated with increased ocean temperature, tends to be accompanied by small body size and reduced fecundity in coho salmon. When all spawners in a time period were females, egg deposition for that time period was zero. No adjustment was made for the infrequent high female to male sex ratios. Mathisen (1962) found no difference in egg mortality that could be attributed to sex ratios as high as 15 females per male in sockeye salmon, *Oncorhynchus nerka*, much higher than would typically be drawn from a binomial distribution.

Moring and Lantz (1975) estimated no fry emerge from about 15% of coho salmon redds, likely the result of gravel scouring (Koski 1966). We reduced egg deposition to account for this mortality by assuming one redd per female and drawing the number of successful redds in each reach from a binomial distribution where $p = 0.85$ and n is the number of females. Egg deposition from the three time periods was summed to arrive at a total number of eggs in each reach.

Summer parr

The number of summer parr in each reach was calculated by multiplying egg deposition (D) by an egg-to-parr survival rate

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(S_{parr}), which was estimated from a density-dependent function based on the relative level of seeding (P), where

$$(1) \qquad P = D/D_m$$

and D_m is the egg deposition needed to produce maximum smolts from the reach as estimated using the habitat model of Nickelson (1998).

Relative seeding level was used as an independent variable to estimate egg-to-parr survival rate because each reach had a different productive capacity. Thus, a given number of eggs would represent a different level of seeding in each reach and therefore a different point on a density-dependent curve. The relationship between relative seeding level and egg-to-parr survival rate, based on data from Moring and Lantz (1975) and Hall et al. (1987), yielded the following equation ($r = 0.762$, $p < 0.001$):

$$(2) \qquad S_{parr} = 0.079P^{-0.699}e^{E}$$

from a functional regression of $\log_e S_{parr}$ on $\log_e P$ (Peterman 1981). The annual E value is used to represent variability due to basin-wide environmental factors (although measurement error is also included in the original data), such as extreme flows, that could affect survival uniformly across reaches. Survival rates differed among reaches because of differences in juvenile density. In the model, E was calculated each year by multiplying the standard deviation of the residuals from the fit of eq. 2 by a value chosen randomly from a standard normal distribution. The fitted curve resulted in survival rates >100% when seeding level was <3.7%, so egg-to-parr survival rate was capped at 44%, the highest observed in the data set. The lognormal form of the deviation term also had a tendency to produce unrealistically high survival rates all along the curve. To constrain modeled variability, the maximum random value chosen from the standard normal distribution was set at 0.946. This resulted in limiting the upper extreme of variability to a value consistent with the maximum positive residual actually observed in the data set.

Genetic effects

At this point in the life history, we applied a factor to account for genetic effects of small spawner population size. When effective population size (N_e) is small, generally on the order of 100 individuals or less, genetic fitness is reduced because deleterious mutations accumulate due to random genetic drift (Lynch 1999). When N_e is relatively large (≥ 1000 individuals), genetic reduction in fitness is generally not a problem. This reduction in fitness is in the range of 1.5% per generation at very low N_e and is cumulative (Lynch 1999). A conservative estimate of N_e is about 20% of the actual number of spawners (Lynch 1999). Because there is genetic interaction among successive broods of coho salmon, through mixing of age 2 jacks, age 3 adults, and age 4 adults, N_e can be approximated by

$$(3) \qquad N_e = 0.2 \times 3N_i$$

where N_i is the number of spawners in a basin in year i as determined by summing spawner populations across reaches. We modeled reduction in fitness (f) as a reduction in survival rate and describe the portion attributable to any given generation by assuming (*i*) $f = 0$ when $N_e \geq 1000$, (*ii*) $f = 0.001$ when $N_e = 100$, (*iii*) $f = 0.015$ when $N_e = 5$, and (*iv*) the change in f is linear between $N_e = 5$ and $N_e = 100$ and between $N_e = 100$ and $N_e = 1000$ (M. Lynch, University of Oregon, Eugene, Oreg., personal communication).

The cumulative effect through time of deleterious mutations (g) can be expressed as

$$(4) \qquad g_i = (1 - f_1)(1 - f_2)(1 - f_3)\ldots(1 - f_i)$$

In the model, g_i was multiplied by the egg-to-parr survival rate to effect a reduction in survival.

This model of genetic effects was intended to capture, in a very general way, one aspect of genetics that could be important at low population sizes. We have not accounted for genetic diversity among populations in any way. The process of natural selection would be expected to reduce effects of inbreeding depression over time. We chose not to model natural selection because it is thought to operate on a longer time frame than inbreeding depression, we have little information to model the effect, and we wanted the model predictions to err on the side of low population numbers. Other efforts are underway to model genetic risks to salmon populations (M. Lynch, University of Oregon, Eugene, Oreg., personal communication).

Smolts

The number of smolts in a reach was calculated by multiplying summer parr by a reach-specific overwinter survival rate as described by Nickelson (1998). The overwinter survival function was

$$(5) \qquad S_{ow} = 0.1361\log_e C + 0.487 + E$$

where S_{ow} is overwinter survival rate and C is estimated smolt capacity (smolts per square metre) ($r = 0.806$, $p < 0.001$). As with egg-to-parr survival, annual deviation from the regression (eq. 5) was modeled as variation due to environmental patterns, such as rainfall, that affect the basin uniformly. The deviation term for a given year was calculated as the standard deviation of the observed residuals from eq. 5 multiplied by a value chosen randomly from a standard normal distribution. The value for the overwinter survival rate for a reach in a given year was derived by adding the annual deviation term to the value of S_{ow}. This deviation term, like the egg-to-parr deviation term, has a tendency to produce unrealistically high survival rates. To curb this tendency, the maximum random value chosen from the normal distribution was 2.260. This confined the variability in maximum survival rates to a range consistent with the maximum positive residual observed in the data. Smolt number for a given reach was capped at M. When calculated survival values were <0, they were set to 2.5%, the lowest actual value observed.

Adults

The number of adults from each reach was determined using a binomial distribution where n is the number of smolts and p is a marine survival rate incorporating environmental variability. For the purpose of this model, marine survival was defined as the period encompassing downstream smolt migration from the natal stream and ocean residence until their second summer. Harvest of adults was modeled from a binomial distribution where n is the number of adults and $p = 1$ minus the fishery exploitation rate. Adults remaining after harvest returned as spawners, as additional natural mortality on adults was assumed to be negligible.

Spawners

As spawners entered a basin, they returned to their natal reaches with a 5% within-basin straying rate. The straying rate was applied in the form of two components: (*i*) fish left a reach randomly with a binomial probability distribution where $p = 0.05$ and n is the number of spawners returning to that reach and (*ii*) fish that have left a reach select a new reach at random with equal probability for all reaches. The effect was to redistribute 5% of the spawners each generation, permitting repopulation of reaches where spawners had gone locally extinct. Labelle (1992) found that straying of wild adult coho salmon among Vancouver Island tributaries to the Strait of Georgia ranged from 0 to 7.8% and averaged 4.2% one year, 0% a second year, and 2.1% overall. The value we used for within-basin straying was roughly double Labelle's among-basin rate be-

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cause we judged that straying within a basin was apt to be greater than straying between basins.

Simulations

Monte Carlo trials of 1000 iterations were conducted for individual river basins, recording the coho salmon population size for the basin each generation. Median ending population, probability of population decline, and probability of extinction for a single brood were calculated from the results of each trial. Because of uncertainty of demographic effects at low population sizes, quasiextinction (Ginzburg et al. 1982), hereafter referred to as extinction, was defined to occur in a given iteration if a spawning population size ≤50 occurred for a basin at any time during the 30 or 99 years modeled. Confidence intervals for extinction probabilities were estimated using the bootstrap method of Willemain (1994). Three coastal basins were chosen for these trials. The basins represented high (Yaquina Basin), medium (Coos Bay Basin), and low (Tillamook Bay Basin) levels of habitat quality (Nickelson 1998).

The Tillamook Bay Basin (Tillamook Basin) (45°30′N) comprises five major rivers and 249 miles of coho salmon habitat. The basin covers about 10 600 km^2, much of which burned in the late 1930s and 1940s. The Yaquina Basin (44°36′N) is a small basin (about 4600 km^2) and includes 109 miles of coho salmon habitat. The Coos Bay Basin (Coos Basin) (43°24′N) covers about 11 300 km^2 and contains 208 miles of coho salmon habitat. All three basins have large estuaries. The three watersheds have experienced similar land uses since the turn of the century (Lichatowich 1989).

Each basin was defined from a set of stream reaches surveyed for habitat quality (Moore et al. 1995). A starting spawner population number was specified for each reach. The distribution of the starting population across reaches was dependent on the quality of habitat in each reach because the capacity of a given reach to support coho salmon varied with habitat quality. This distribution was derived as the equilibrium distribution of spawners at the marine survival rate that produced the desired total population size. Using 1995 population levels, this method produced frequency distributions of spawner densities that were not significantly different (Wilcoxon signed-rank test, $p > 0.5$) from frequency distributions of actual spawner densities estimated from spawner surveys conducted in the three basins (ODFW, unpublished data).

The stream reaches used in the model represented 36, 57, and 25% of available coho salmon habitat in the Tillamook, Yaquina, and Coos Basins, respectively. To simulate effects of low spawner densities and straying, we needed a representation of all reaches in each basin. We assumed that the distribution of habitat qualities in the sampled reaches was representative of the basin. The total number of reaches present in each basin was calculated from the sampling fraction. The unsampled fraction of reaches was chosen from the sample randomly, with replacement. The bootstrap sample was repeated for each iteration of the model (Efron and Tibshirani 1986). In this way, uncertainty arising from sampling variability in the habitat data was incorporated in the range of modeled results.

Marine survival

There are no direct measures of marine survival available for wild coho salmon from Oregon. However, data from coastal Washington for the 1980s (Seiler 1989) suggest that marine survival of wild smolts was about double that of hatchery smolts. Nickelson (1986) provided evidence to suggest that wild smolts from the Oregon coast survived about as well as Columbia River hatchery smolts during periods of strong upwelling, but when upwelling was weak, wild smolts survived better than hatchery smolts. Oregon coastal and Columbia River hatchery data show smolt-to-adult survivals ranging from 0.12 to 11.0% for brood years 1958–1992 with a mean of 3.7%. Earlier brood years (1958–1974) had a higher average survival of 6.25%, while later years (1975–1992) had a lower survival of 1.57%. The most recent years of 1980–1992 had an average survival of 0.83%. Coefficients of variation depended on time period and ranged from 0.4 for the 1958–1974 period to 1.06 for the 1975–1992 years. Distributions of survival within these time periods approximated gamma distributions (Rubinstein 1981; Ratner et al. 1997) defined by mean and coefficient of variation. We used gamma distributions from within the observed range of survivals in our model runs.

Thirty-year trials

Thirty-year trials were used to test the sensitivity of our model to assumptions of marine survival and exploitation rate. We tested three different levels of average marine survival. The rate for a given year was taken from a gamma distribution with an average (coefficient of variation) typical of those observed during periods of high, medium, and low marine survival since 1970 (PFMC 1998). Values tested were 6% (0.4472), 3% (0.5774), and 1.5% (0.5774).

We tested exploitation rates of 0, 20, 40, 60, and 80%. With the exception of 0%, these rates are typical of harvest levels experienced over the past three decades (PFMC 1998). This range was used to describe the relationship between exploitation rate and measures of persistence at each level of marine survival. Initial populations for these trials were set at 1000 spawners.

Ninety-nine-year trials

Ninety-nine-year trials were used to examine the long-term risk of extinction of Oregon coastal coho salmon populations. Marine survival followed a cyclic pattern in these trials. Annual exploitation rate was based on marine survival and parental escapement to approximate the harvest strategy proposed for coho salmon (ODFW 1997).

For the long-term simulations, it was necessary to take into account the cyclic nature of climate (i.e., regime shifts) and the marine environment (Beamish and Bouillon 1993). To accomplish this, we used the Aleutian low pressure index (ALPI) (Beamish and Bouillon 1993) as a template for the pattern of long-term climatic variability. This annual index represents the intensity of the low-pressure system over the northern North Pacific Ocean during winter and spring (December–May) for the years 1900–1989. Beamish and Bouillon (1993) noted a strong positive correlation between ALPI and salmon production in the Gulf of Alaska. Typically, production of coho salmon in Oregon has been inversely correlated with production of coho salmon in Alaska (Nickelson and Lichatowich 1984). Thus, when ALPI is low, survival of coho salmon in Oregon has been generally high, and when ALPI is high, survival has been generally low. For modeling purposes, the long-term cyclic pattern of ALPI was approximated by a step function developed by dividing the smoothed trend (9-year running average) by a constant and converting to an integer. Average marine survival rates (coefficients of variation) of 6% (0.4472), 4.5% (0.5000), 3% (0.5774), and 1.5% (0.5774) were assigned to the resulting steps of 0–3, respectively. Since the database runs for only 89 years, it was doubled by appending the first year to the last year.

Because we are currently experiencing low survival conditions, simulations began with a randomly chosen year j having a step value of 3 (1.5% survival) and with year $j + 3$ also having a step value of 3. For each subsequent generation of the simulation, the model proceeded through the ALPI cycle using the value of year $j + 3, j + 6, \ldots j + 99$, taking survival rates from a gamma distribution with appropriate mean and coefficient of variation.

Exploitation rates of 15, 20, 25, and 35% were linked to marine survivals of 1.5, 3, 4.5, and 6%, respectively. If total parental spawner abundance was <50% of full seeding of the best habitat in the basin (Nickelson 1998), the lowest exploitation rate was ap-

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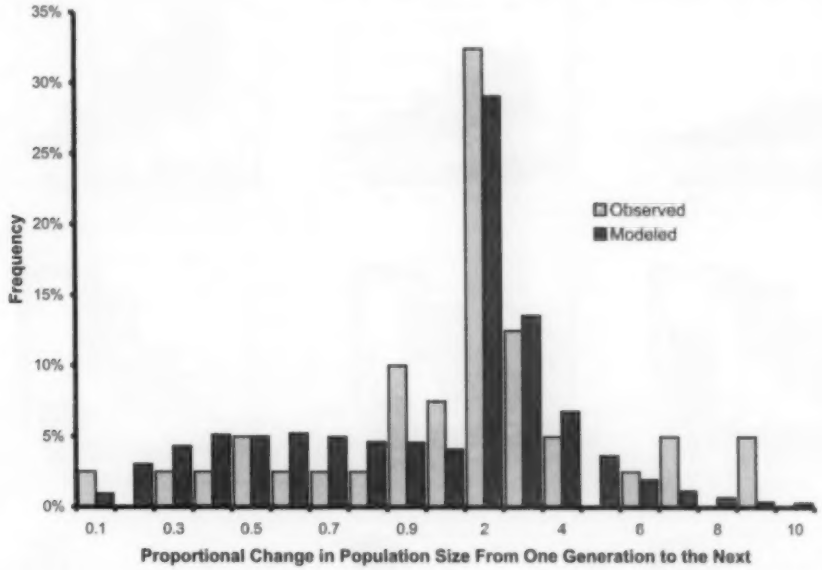
Fig. 1. Frequency distribution of proportional change in population size from one generation to the next based on results from the simulation model (three basins, 99 000 observations) and on observed spawner abundance in 11 Oregon coastal basins between 1990 and 1996.



plied (ODFW 1997). The highest exploitation rate was applied only when parental spawner abundance exceeded 75% of full seeding of the best habitat in the basin.

We examined the effect of coho salmon population size in a basin on the probability of extinction by modeling a range of initial population sizes. Starting populations of about 100, 200, 300, 400, 600, 1000, and 1500 were used for each of the three basins.

The trials described so far are based on current habitat quality remaining constant for the next century. It is unrealistic to expect this to be the case. However, it is also uncertain what the trajectory of habitat change over the next century will be. Habitat change was modeled as an exponential function that resulted in a specified change (ΔH) in habitat quality (H) over the period of 99 years. Trials were run for changes in H of +20, 0, –20, –40, and –60% over the next century. Each generation, the smolt capacity of each reach (the surrogate for habitat quality) was increased or decreased by multiplying C by e^a where $a = \ln \Delta H/(\text{no. of generations} - 1)$. The estimated spawner population in each basin in 1995 (ODFW, unpublished data) was used as a starting point for these simulations. Starting populations were 300 for the Tillamook Basin, 5700 for the Yaquina Basin, and 10 400 for the Coos Basin.

Results and discussion

Model

Four types of population stochasticity that should be accounted for in a PVA are environmental, demographic, genetic, and catastrophic (Shaffer 1981; Thompson 1991). We include the first three with specific functions in our model. Catastrophic variability was not explicitly addressed. However, very low survival rates did occur infrequently in the simulations as a result of the random variation built into the model. These very low survival rates could be viewed to be the result of catastrophic events because they had the effect of eliminating populations in certain reaches.

Quantitative results from this model depend on our estimates of a variety of parameters and processes. These include habitat carrying capacity, survival rates at various life history stages, the shapes of density-dependent survival functions, straying rates, and the structure of variability in egg-to-parr, overwinter, and marine survival. Inaccuracies in our estimates of these factors affect the numerical predictions of the model. However, all of the parameters and functional relationships in the model are based on data from studies of coho salmon.

During the course of model development, outputs were compared with known values and our understanding of the behavior of these systems, so that we are confident that the numerical outputs are in the correct range. For example, frequency distributions of spawner densities produced by the model were similar to those actually observed. Also, the distribution of proportional change in population size from one generation to the next in the simulation results was not significantly different (Wilcoxon signed-rank test, $p > 0.2$) from that observed in wild coho salmon populations in Oregon coastal basins over the period 1990–1996 (Fig. 1). In wild populations, declines were observed 37.5% of the time compared with 42.0% in simulations. Wild populations increased by less than twofold in 32.5% of observations and 29.1% of simulations. Virtually all observed and modeled changes were in the range of ±10-fold. If anything, the model tended to produce a greater percentage of declining populations than was actually observed. This indicates that the model may be conservative in estimating extinction probabilities.

Thirty-year simulations

The 30-year simulations were used to test the sensitivity of similar starting populations in three basins with different habitat qualities to a range of marine survival rates and ex-

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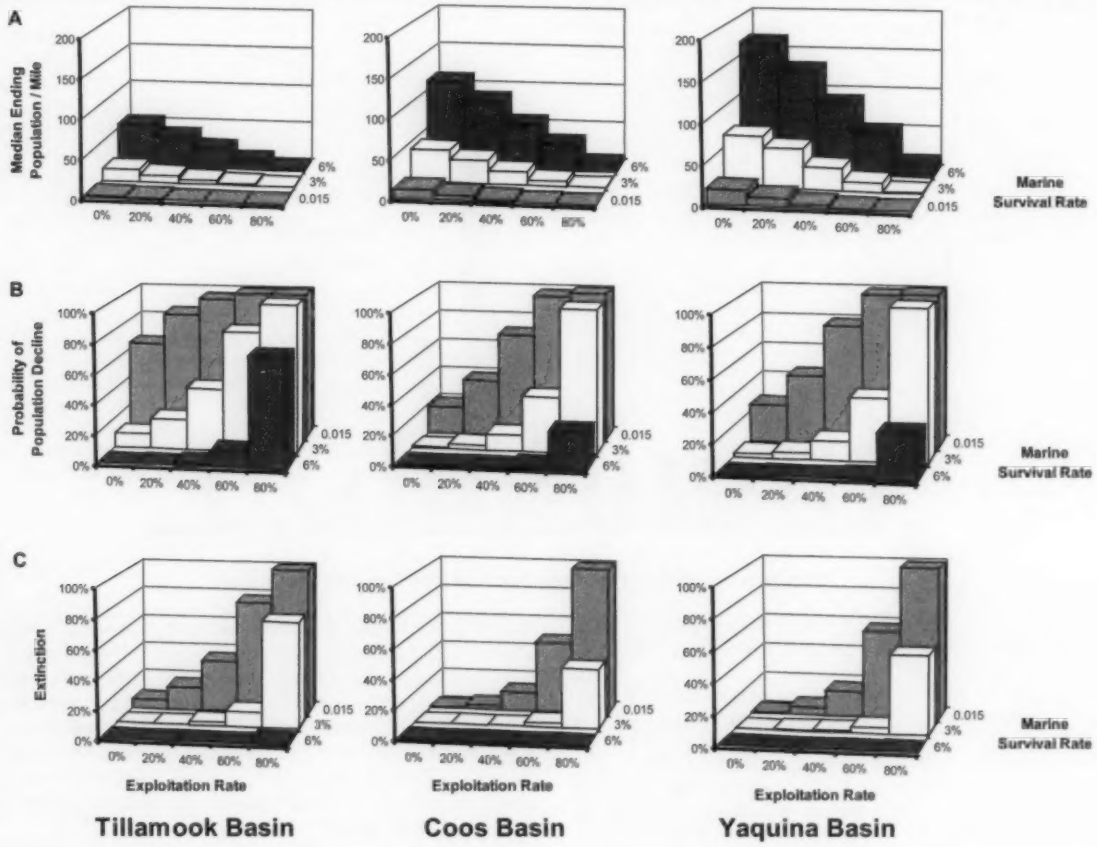
Fig. 2. Results of 10-generation model simulations comparing different levels of marine survival and exploitation rate. (A) Median ending population per mile of habitat; (B) probability of population decline over the 10 generations; (C) probability of extinction.



ploitation rates. The pattern of effects of marine survival and exploitation were similar for all three basins, differing only in magnitude (Fig. 2). Median ending population per mile of habitat after 30 years, probability of population decline, and probability of extinction were all strongly influenced by marine survival and exploitation rate, alone and in combination. Effects of decreased marine survival or increased exploitation rate were correlated with habitat quality, being greatest in the Tillamook Basin, least in the Yaquina Basin, and intermediate in the Coos Basin.

These simulations suggest that exploitation rates of 40% will result in significant probability of population decline in basins with poor habitat, such as the Tillamook, when marine survival is 3% (Fig. 2). If marine survival of wild fish is about twice the rate of hatchery fish, 3% survival would be similar to the average since 1975. When marine survival rate was set at 1.5%, there was at least 20% probability of population decline even with zero exploitation. Under these conditions, a 20% exploitation rate resulted in a 16% probability of extinction of the Tillamook population within 30 years.

Ninety-nine-year simulations: viability of Oregon coastal coho salmon

The 99-year simulations were used to examine the longer term viability of Oregon coastal coho salmon populations. The primary difference between the 30-year simulations and the 99-year simulations was the cyclic nature of marine survival used in the longer runs. We examined beginning populations that ranged from 100 to 1500 spawners in each of the three basins. The effect of beginning population size on median ending population depended on the quality of habitat in the basin. In the Yaquina Basin (best quality habitat), all starting populations had similar median ending populations (Fig. 3). In the Coos Basin (intermediate quality habitat), starting populations of 150 and greater had similar median ending populations (Fig. 3). In the Tillamook Basin (poorest quality habitat), starting populations of 200 and greater had similar median ending populations (Fig. 3).

In these simulations, the risk of extinction (≤ 50 spawners at any time) increased gradually as starting populations decreased from 1500 to 300 and increased rapidly as starting populations dropped below 300 fish in each basin (Fig. 3). However, only in the Tillamook Basin was the 5% standard for risk of extinction approached or exceeded when starting populations were $\geq$300 fish. Estimates of spawning populations in these basins for 1994–1996 have been about 900, 300, and 700 in the Tillamook Basin, 2400, 5700, and 5100 in the Yaquina Basin, and 14 600, 10 500, and 12 100 in the

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Fig. 3. Median population size and mean probability of extinction (with 95% confidence intervals) from simulations of 33 generations with different levels of starting population for the (A) Tillamook, (B) Yaquina, and (C) Coos basins.

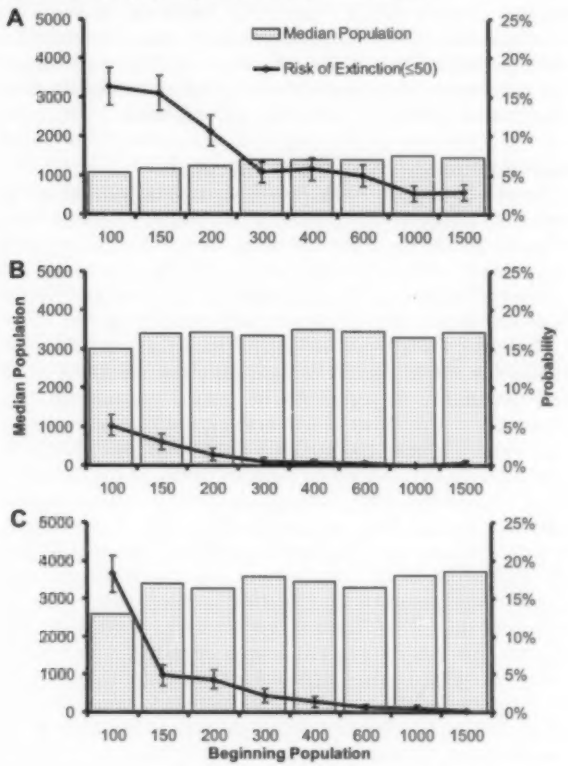
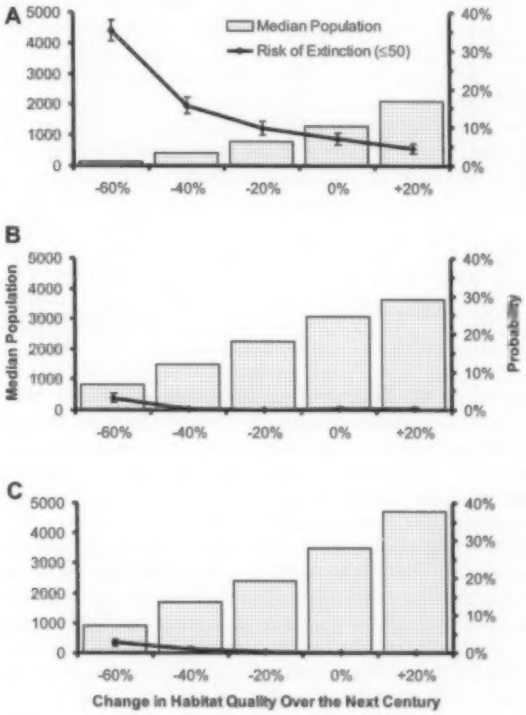


Fig. 4. Median population size and mean probability of extinction (with 95% confidence intervals) from simulations of 33 generations with different levels of change in freshwater habitat quality for the (A) Tillamook, (B) Yaquina, and (C) Coos basins.



Coos Basin (Nickelson 1998). Populations in the Yaquina and Coos basins are well above the level where we found a significant risk of extinction. However, in the Tillamook Basin, all three cycles are at, or near, abundance levels that would be considered at moderate risk of extinction (Allendorf et al. 1997).

The above results assume that current habitat quality would be maintained for the next 99 years. We also examined the effects of changes in habitat quality, ranging from a 20% increase to a 60% decrease over the next century, on the median ending population and probability of extinction. We used starting populations equivalent to the 1995 levels in each basin. Lawson (1993) predicted that a declining trend in habitat quality over several cycles in marine productivity would result in increasing likelihood of extinction during low-productivity phases of the climate cycle. Our simulations show a substantial increase in the risk of extinction ($p \leq 0.05$) in basins with poor-quality habitat, such as the Tillamook, if habitat quality over the next century were to decline by 20% or more (Fig. 4). Based on an evaluation of habitat quality by Nickelson (1998), this would probably apply to the Nestucca Basin as well. Similar declines in the quality of habitat in the remaining major coastal basins would have a lesser effect on the sustainability of coho salmon populations, as illustrated by the results for the Yaquina and Coos basins (Fig. 4), where significant increased risk of extinction did not occur until habitat had declined by 60% ($p \leq 0.05$). In these basins, loss of habitat quality had little effect on population viability because there were enough good-quality reaches to maintain the population during periods of poor marine survival. This was not the case for the Tillamook Basin.

Whereas decreased habitat quality significantly affected population viability only in the basin with the poorest habitat (Tillamook), the effect on median population size after 99 years was similar for all three basins tested, although it was somewhat more pronounced in the Tillamook Basin (Fig. 4). Percentage decreases in population size were consistently greater than the percentage decreases in habitat quality. For example, 60% reduction in habitat quality resulted in 73, 74, and 89% reductions in median population size in the Yaquina, Coos, and Tillamook basins, respectively. These results provide a clear case for protection of existing habitat to prevent further decreases in habitat quality. Further loss of habitat would result in significant decreases in population size, which could lead to increased risk of extinction, particularly in basins with poor-quality habitat.

Improvement in habitat quality by 20% resulted in increased median population size in all three basins, but was not quite enough improvement to result in significant decreases in probability of extinction in the Tillamook Basin (Fig. 4). The largest percentage gain in median population

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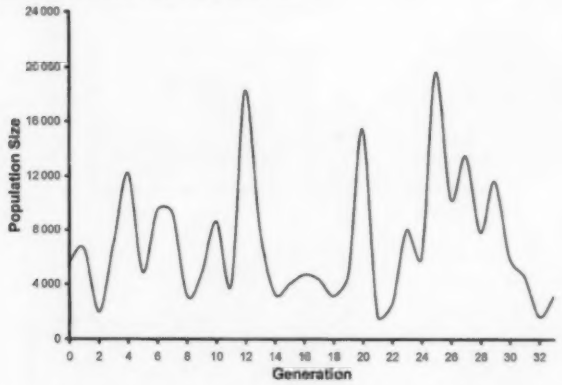
Fig. 5. Typical example of simulated time series of population size from a single 33-generation trial for the Yaquina Basin. The trial started with the 1995 estimated population, and freshwater habitat condition was held constant.



size was in the Tillamook Basin, where a 20% increase in habitat quality resulted in a 62% increase in population size. This result suggests that if effective habitat restoration activities were undertaken, significant increases in long-term population abundance could be realized, even in basins with very poor habitat and a small population.

The fine-grained habitat structure of the model provided insights into the dynamics of coho salmon populations and the mechanisms controlling their distribution within a basin. The long-term cyclic variation in marine survival (climate) that was built into the model caused population abundance in a basin to fluctuate through time (Fig. 5). Populations in reaches with the best habitat tended to persist through the ups and downs of the climatic cycle. Populations in reaches with poor-quality habitat tended to become extinct during periods of poor marine survival. During periods of favorable marine survival, the high productivity reaches served as sources for recolonization of the lower quality reaches through the mechanism of straying. As a result, population size and distribution within a basin expanded and contracted through time. Within a reach, populations were resilient unless numbers dropped to a level where demographic risk factors became more important than density-dependent population dynamics. Persistence of populations in a basin during periods of poor marine survival depended on the highest quality reaches. Results suggest that there is some threshold proportion of the habitat in a basin that must remain high quality for a population to have acceptable probabilities of persistence. Such a threshold level could prove useful as a benchmark for assessing the status of freshwater habitat through time. Further analysis of additional coastal basins would be needed to define the habitat threshold.

The results of our analysis suggest that the status of coho salmon populations in most major Oregon coastal basins over the next 100 years is largely dependent on the quality of freshwater habitat and survival in the marine environment and is relatively independent of the current population size. Exceptions may be basins such as the Tillamook, where freshwater habitat is poor and populations have dropped below a few hundred fish in recent years. Evaluations of extinction risks over 99 years are based on the assumption that the marine environment in the next century will be similar to the past century. Since about 1983, there seems to have been a change in the relationship between coho salmon survival in Oregon and indices of marine environment such as upwelling (Pearcy 1997). Since 1992, there has been an extended series of low-survival years for most Oregon coho salmon populations. If the long-term cycles have changed for the worse, then our viability projections, sensitive as they are to marine survival, may be optimistic.

Model limitations and future directions

In developing this model, we have tried to incorporate, as much as possible, the dynamics of Oregon's coastal coho salmon. Inevitably, there are areas where the model could use further refinement. We identified three such areas: improved parameter estimation, influences of hatchery fish on wild production, and a more explicit spatial structure.

Variability is integral to natural processes. We have attempted to model aspects of variability that are likely to affect probability of persistence in natural populations. Our treatment of variability is exploratory and limited by available data. We have modeled the error structures of egg-to-parr survival and overwinter survival based on the statistical fit of regressions. Two components of error in these regressions are process error and measurement error. Process error, in turn, operates at a variety of spatial and temporal scales. We have assigned all variability in our regressions to interannual variation operating uniformly within a basin. This almost certainly overestimates between-year variability and ignores finer scale variations among populations in a basin. Although not the most elegant of approaches, the truncation of maximum values and setting of minimum values for survival of these two life stages was an attempt to maintain the magnitude of variation within reasonable limits and prevent rare occurrence of unrealistic results, such as 100% survival at full seeding. Process error is likely to be correlated among life stages. Thus, egg-to-parr survival, overwinter survival, and marine survival could covary. In addition, there is probably autocorrelation in the covariance time series. Our 99-year simulations modeled marine survival on a template of long-term climate cycles, thereby incorporating time series covariance. Part of the variability in other life history parameters could also be linked to climate cycles. Progress in improving our treatment of variation will depend on our ability to partition error more finely and on improved understanding of environmental effects (e.g., rainfall, temperature, and upwelling) on salmon survival at different life stages. As our understanding of patterns in variability improves, we will continue to refine its representation in the model.

Hatchery-reared smolts have been a feature of Oregon coastal basins for over a century. Hatcheries, and hatchery fish, can affect wild fish survival in a variety of ways at different stages of the life cycle. Smolts may compete for food or space in estuaries and the nearshore ocean. They may also affect predator–prey dynamics, or serve as reservoirs of disease. Hatchery adults on spawning grounds may displace wild spawners, interfere with natural selection and gene flow (thereby reducing fitness), or result in increased juvenile densities that reduce overall egg-to-smolt survival. We have not included any hatchery effects in our model at this time, primarily because of the difficulty in identifying important

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functional relationships and obtaining suitable data for modeling. It may be, however, that hatcheries are an important factor in the viability of wild coho salmon populations. Incorporation of hatchery influences is an important next step in model development.

We have treated each reach in a basin as equally accessible to fish from all other reaches. The movement of individuals among patches is an important feature of metapopulations (Gilpin 1987). Habitat fragmentation can limit interactions among isolated spawning populations. Migration barriers render areas of suitable habitat inaccessible to spawners or rearing juveniles. The spatial relationship among stream reaches in the stream network affects straying and recolonization rates in ways that have implications for restoration but are not captured in our model. Inclusion of more realistic metapopulation dynamics would allow us to refine our estimates of population viability. Incorporating a spatially explicit structure would also improve the model's usefulness for analyzing alternative management strategies.

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References

Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A., Hankin, D., Lichatowich, J.A., Nehlsen, W., Trotter, P.C., and Williams, T.H. 1997. Prioritizing Pacific salmon stocks for conservation. Conserv. Biol. **11**: 140–152.

Beamish, R.J., and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. **50**: 1002–1016.

Botsford, L.W., and Brittnacher, J.G. 1998. Viability of Sacramento River winter run chinook salmon. Conserv. Biol. **12**: 65–79.

Cooney, C.X., and Jacobs, S.E. 1995. Oregon coastal salmon spawning surveys, 1993. Oreg. Dep. Fish Wildl. Fish. Div. Info. Rep. 95-3.

Efron, B., and Tibshirani, R. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Stat. Sci. **1**: 54–77.

Emlen, J.M. 1995. Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **52**: 1442–1448.

Gilpin, M.E. 1987. Spatial structure and population vulnerability. *In* Viable populations for conservation. *Edited by* M.E. Soulé. Cambridge University Press, Cambridge, U.K. pp. 125–139.

Ginzburg, L.R., Slobodkin, L.B., Johnson, K., and Bindman, A.G. 1982. Quasiextinction probabilities as a measure of impacts on population growth. Risk Anal. **2**: 171–181.

Goodman, D. 1999. Population viability analysis: the risk assessment paradigm. *In* Workshop on Assessing Extinction Risk for West Coast Salmonids, Seattle, Wash., November 13–15, 1996. NOAA Tech. Memo. NMFS. In press.

Hall, J.D., Brown, G.W., and Lantz, R.L. 1987. The Alsea watershed study: a retrospective. *In* Streamside management: forestry and fishery interactions. *Edited by* E.O. Salo and T.W. Cundy. Contrib. No. 57, Institute of Forest Resources, University of Washington, Seattle, Wash. pp. 399–416.

Johnson, S.L. 1988. The effects of the 1983 El Niño on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Fish. Res. **6**: 105–123.

Koski, K.V. 1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. Master's thesis, Oregon State University, Corvallis, Oreg.

Labelle, M. 1992. Straying patterns of coho salmon (*Oncorhynchus kisutch*) stocks from southeast Vancouver Island, British Columbia. Can. J. Fish. Aquat. Sci. **49**: 1843–1855.

Lawson, P.W. 1993. Cycles in ocean productivity, trends in habitat quality, and the restoration of salmon runs in Oregon. Fisheries (Bethesda), **18**(8): 6–10.

Lichatowich, J.A. 1989. Habitat alteration and changes in abundance of coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) in Oregon coastal streams. *In* Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. *Edited by* C.D. Levings, L.B. Holtby, and M.A. Henderson. Can. Spec. Publ. Fish. Aquat. Sci. No. 105. pp. 92–99.

Lynch, M. 1999. The genetic risks of extinction for pacific salmonids. *In* Workshop on Assessing Extinction Risk for West Coast Salmonids, Seattle, Wash., November 13–15, 1996. NOAA Tech. Memo. NMFS. In press.

Mathisen, O.A. 1962. The effect of altered sex ratios on the spawning of red salmon. *In* Studies of Alaska red salmon. University of Washington Press, Seattle, Wash. pp. 139–245.

Moore, K., Jones, K., and Dambacher, J. 1995. Methods for stream habitat surveys, version 5.1. Oreg. Dep. Fish Wildl., Res. Dev. Sect., Corvallis, Oreg.

Moring, J.R., and Lantz, R.L. 1975. The Alsea watershed study: effects of logging on the aquatic resources of three headwater streams of the Alsea River, Oregon. Part I. Biological studies. Oreg. Dep. Fish Wildl. Fish. Div. Fish. Res. Rep. 9.

Murphy, D.D., Freas, K.E., and Weiss, S.B. 1990. An environment–metapopulation approach to population viability analysis for a threatened invertebrate. Conserv. Biol. **4**: 41–51.

Nickelson, T.E. 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production Area. Can. J. Fish. Aquat. Sci. **43**: 527–535.

Nickelson, T.E. 1998. A habitat-based assessment of coho salmon production potential and spawner escapement needs for Oregon coastal streams. Oreg. Dep. Fish Wildl. Fish. Div. Info. Rep. 98-4.

Nickelson, T.E., and Lichatowich, J.A. 1984. The influence of the marine environment on the interannual variation in coho salmon abundance: an overview. *In* The influence of ocean conditions on the production of salmonids in the North Pacific, a Workshop. *Edited by* W.G. Pearcy. Oregon State University Sea Grant College Program, Corvallis, Oreg. pp. 24–36.

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Oregon Department of Fish and Wildlife (ODFW). 1997. Proposed new spawner escapement rebuilding criteria and fishery management regime for Oregon coastal natural (OCN) coho salmon. Report to the Pacific Fishery Management Council. Oreg. Dep. Fish Wildl., Fish. Div., Portland, Oreg.

Pacific Fisheries Management Council (PFMC). 1998. Preseason report I: Stock abundance analysis for 1998 ocean salmon fisheries. Pacific Fisheries Management Council, Portland, Oreg.

Pearcy, W.G. 1997. Salmon production in changing ocean domains. *In* Pacific salmon and their ecosystems: status and future options. *Edited by* D.J. Stouder, P.A. Bisson, and R.J. Naiman. Chapman and Hall, New York. pp. 331–352.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. **38**: 1113–1119.

Ratner, S., Lande, R., and Roper, B.B. 1997. Population viability analysis of spring chinook salmon in the South Umpqua River, Oregon. Conserv. Biol. **11**: 879–889.

Rubinstein, R.Y. 1981. Simulation and the Monte Carlo method. John Wiley & Sons, New York.

Seiler, D. 1989. Differential survival of Grays Harbor basin anadromous salmonids: water quality implications. *In* Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. *Edited by* C.D. Levings, L.B. Holtby, and M.A. Henderson. Can. Spec. Publ. Fish. Aquat. Sci. No. 105. pp. 123–135.

Shaffer, M.L. 1981. Minimum viable population sizes for conservation. BioScience, **31**: 131–134.

Shaffer, M.L. 1990. Population viability analysis. Conserv. Biol. **4**: 39–40.

Thompson, G.G. 1991. Determining minimum viable populations under the Endangered Species Act. NOAA Tech. Memo. NMFS F/NWC-198.

Willemain, T.R. 1994. Bootstrap on a shoestring: resampling using spreadsheets. Am. Stat. **48**: 40–42.

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Effect of individual variability on estimation of population parameters from length-frequency data

You-Gan Wang and Nick Ellis

Abstract: We consider estimation of mortality rates and growth parameters from length-frequency data of a fish stock when there is individual variability in the von Bertalanffy growth parameter L_∞ and investigate the possible bias in the estimates when the individual variability is ignored. Three methods are examined: (*i*) the regression method based on the Beverton and Holt's (1956, Rapp. P.V. Reun. Cons. Int. Explor. Mer, **140**: 67–83) equation; (*ii*) the moment method of Powell (1979, Rapp. P.V. Reun. Int. Explor. Mer, **175**: 167–169); and (*iii*) a generalization of Powell's method that estimates the individual variability to be incorporated into the estimation. It is found that the biases in the estimates from the existing methods are, in general, substantial, even when individual variability in growth is small and recruitment is uniform, and the generalized method performs better in terms of bias but is subject to a larger variation. There is a need to develop robust and flexible methods to deal with individual variability in the analysis of length-frequency data.

Résumé : Nous avons considéré l'estimation des taux de mortalité et des paramètres de croissance à partir de données de fréquence des longueurs pour un stock de poissons dans lequel il y a variabilité individuelle du paramètre de croissance L_∞ de von Bertalanffy, et examiner le biais possible dans les estimations quand la variabilité individuelle est ignorée. Trois méthodes sont examinées : (*i*) la méthode de régression fondée sur l'équation de Beverton et Holt (1956, Rapp. P. V. Réun. Cons. Int. Explor. Mer, **140** : 67–83); (*ii*) la méthode des moments de Powell (1979, Cons.Int. Explor. Mer, **175** : 167–169); et (*iii*) une généralisation de la méthode de Powell qui estime la variabilité individuelle à incorporer dans l'estimation. Nous avons trouvé que les biais dans les estimations des méthodes existantes sont généralement substantiels, même quand la variabilité individuelle de la croissance est faible et que le recrutement est uniforme; en outre, la méthode généralisée donne de meilleurs résultats au chapitre du biais, mais donne aussi une plus grande variation. L'élaboration de méthodes robustes et souples pour composer avec la variabilité individuelle dans l'analyse des données de fréquence de longueurs s'avère nécessaire.

[Traduit par la Rédaction]

Introduction

Stock assessment plays an important role in making decisions for management of fisheries. Stock assessment relies, to a great extent, on the knowledge of growth and mortality parameters. Length-frequency based methods are important for estimating population parameters when aging is either not possible or very expensive.

Traditional methods assume a deterministic relationship between size and age for the population. It is more realistic to assume there is individual variability in growth (Sainsbury 1980). For example, using tag–recapture data, Wang et al. (1995) found substantial individual variability for the tiger shrimp, *Penaeus semisulcatus*.

Although it is well understood that variability leads to increased uncertainty in estimates, it is less well recognized that variability can also lead to bias, particularly in the analysis of length-frequency data. It is therefore of interest to investigate the effect of individual variability.

In this paper we describe two existing methods (regression and Powell's method) and a modified Powell's method that takes individual variability into account. The objective of this paper is to investigate the bias in these methods resulting from individual variability in growth. The methods are evaluated in a simulation study using a model that incorporates individual variability. The aspects we focus on are the bias and variability of the estimates and the robustness to violations of distributional assumptions.

Estimation methods

We assume that the growth of individuals follows a von Bertalanffy curve so that the length at age a is given by

$$(1) \qquad L(a) = L_\infty(1 - e^{-ka})$$

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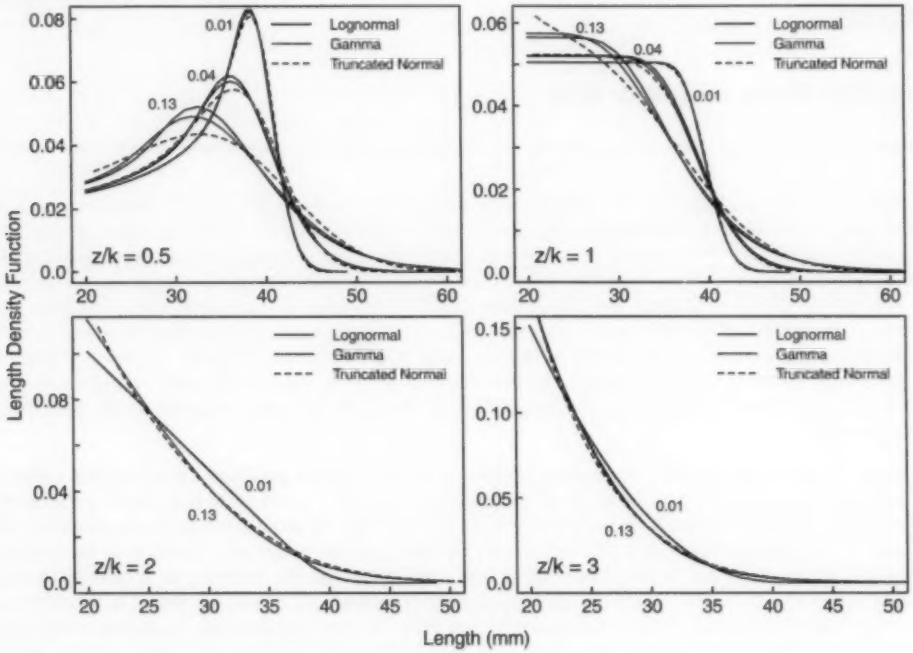
Fig. 1. Length-density functions for the case of constant fixed-length recruitment and constant mortality. Each plot corresponds to a different value of $\theta = z/k$. We use the values 0.5, 1, 2, and 3, as studied by Powell (1979). Groups of curves within a plot are labeled by the value of the coefficient of variation of L_∞. Each group consists of a curve from each of the three distributions as shown in the legend. The recruitment length is 20 mm.



We also assume that the population undergoes constant mortality z. A few methods are available to estimate the ratio $\theta = z/k$, a key parameter in population dynamics. These methods, based on Beverton and Holt (1956), assume that recruitment is continuous and constant throughout the year, leading to a population with an exponentially distributed age structure with mortality as the parameter of the distribution. Under this assumption, the length-frequency distribution is expected to have declining proportions over sizes.

Regression method

Beverton and Holt (1956) first derived an expression for estimating z from length-frequency data and growth parameters (k, l_∞),

$$(2) \qquad z = k\frac{l_\infty - \bar{L}}{\bar{L} - L_m}$$

where $\bar{L}$ is the mean length of individuals with length above the L_m, and L_m is a truncation length such that individuals with length above L_m are fully vulnerable to the fishing gear. This method was established under the assumption that all individuals follow the same von Bertalanffy growth curve.

The Beverton–Holt equation (eq. 2) can be rearranged into the following regression form:

$$(3) \qquad \bar{L} = \alpha + \beta L_m$$

where $\alpha = l_\infty/(1 + \theta)$ and $\beta = \theta/(1 + \theta)$. Estimates of α and β can be obtained by regressing $\bar{L}$ on different L_m values. A weighting function that takes account of correlations between the observed means may be used to improve the estimation efficiency (Wetherall et al. 1987). However, we will simply take the number of fish used to calculate the mean as the weight in the regression. If $\hat{\alpha}$ and $\hat{\beta}$ are the estimates so obtained, we can estimate l_∞ and θ by

$$\hat{\theta} = \frac{\hat{\beta}}{1-\hat{\beta}} \text{ and } \hat{l}_\infty = \frac{\hat{\alpha}}{1-\hat{\beta}}$$

Powell's two-moment method

Powell (1979) first examined the effect of variability in L_∞ on the estimates of θ assuming constant recruitment and constant mortality. We denote the density function of L_∞ as $p(x)$, which has a mean of l_∞ and a variance of σ^2.

If all the recruits have the same size l_0 and mortality is constant, then the density function of L, $f(l)$, satisfies

$$(4) \qquad f(l) = \theta\int_l^\infty \frac{(x-l)^{\theta-1}}{(x-l_0)^\theta}\, p(x \mid L_0 = l_0)\, dx$$

The derivation is given in Appendix 1 (see also Powell 1979). In this case, we can just write $p(x|L_0 = l_0)$ as $p(x)$, which represents the distribution of the maximum length of an individual with recruitment length l_0. Note that, under this model, recruitment of individuals with length L_m ($>l_0$) is also constant. Figure 1 shows examples of some length density functions for several values of σ^2 and various distributions of L_∞.

The moments of the length distribution about l_0 satisfy

$$(5) \qquad \begin{aligned} m_n &= \mathrm{E}\{(L-l_0)^n\} \\ &= \frac{\Gamma(n+1)\Gamma(\theta+1)}{\Gamma(n+\theta+1)}\,\mathrm{E}\{(L_\infty - l_0)^n\}, \end{aligned}$$

where E denotes expectation. Note that the moments of the length distribution are simply proportional to the moments of the L_∞ distribution, with constant of proportionality dependent on θ. The first moment estimation equation ($n = 1$) is equivalent to the Beverton–Holt equation (eq. 2) with $L_m = l_0$. However, when $L_m > l_0$, eq. 2 is

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Table 1. Properties of the lognormal, gamma, and truncated normal distributions, which are candidate distributions for the von Bertalanffy parameter L_∞.

	Lognormal	Gamma	Truncated normal
Properties of the L_∞ distribution			
$p(y\|l_0)$*	$\frac{\phi(\sigma^{-1}[\ln(y-l_0)-\mu])}{y-l_0}$	$\frac{(y-l_0)^{\alpha-1}e^{-(y-l_0)/\beta}}{\beta^\alpha\Gamma(\alpha)}$	$\frac{\phi(\sigma^{-1}(y-\mu))}{\Phi_c(x_0)}$
ρ^2	$e^{\sigma^2}-1$	$1/\alpha$	$1/G_0^2 - x_0/G_0 - 1$
μ_i	$e^{i\mu}e^{(i\sigma)^2/2}$	$\frac{\Gamma(\alpha+i)\beta^i}{\Gamma(\alpha)}$	See eq. A4
Parameter 1	$\sigma^2 = \ln(1+\rho^2)$	$\alpha = 1/\rho^2$	$\sigma = \mu_1/G_0$
Parameter 2	$\mu = 0.5\ln\frac{\mu_1^2}{1+\rho^2}$	$\beta = \mu_1\rho^2$	$\mu = l_0 - \mu_1 x_0/G_0$
Estimates from moments of length distribution			
$\hat\rho^2$	$\frac{\frac{1}{2}M_2}{1-\sqrt{1-\hat\tau}} - 1$	$\frac{M_3+M_2-4}{2(2-M_3)}$	$1/\hat G_0^2 - \hat x_0/\hat G_0 - 1$
$\hat\theta$	$\sqrt{\frac{1}{1-\hat\tau}} - 2$	$\frac{3M_2+M_3-2M}{M-M_2-M_3}$	$\frac{M_2\hat G_0^2 + \hat x_0\hat G_0 - 1}{1-\hat x_0\hat G_0 - \frac{1}{2}M_2\hat G_0^2}$
$\hat l_\infty - l_0$	$\hat m_1\left(\sqrt{\frac{1}{1-\hat\tau}}-1\right)$	$\hat m_1\left(\frac{4M_2+2M_3-3M}{M-M_2-M_3}\right)$	$\frac{\frac{1}{2}\hat m_1 M_2\hat G_0^2}{1-\hat x_0\hat G_0 - \frac{1}{2}M_2\hat G_0^2}$

Note: Estimates are given in terms of the moment estimates $\hat m_i$ and dimensionless quantities derived from them: $\hat\tau = 3\hat m_2^3/4\hat m_3\hat m_1^3$, $M_2 = \hat m_2/\hat m_1^2$, $M_3 = 3\hat m_2^2/\hat m_1\hat m_3$, $M = M_2M_3$, and $\hat G_0 = G(\hat x_0)$. For definitions of μ_i, G, x_0, and $\hat x_0$, see text.

*Density function at $L_\infty = y$.

no longer valid because of the conditioning of the distribution of L_∞ on L_m (see Discussion).

Powell (1979) used the first two moment equations to obtain

$$(6)\quad \begin{cases} \theta = \dfrac{2(m_2 - (1+\rho^2)m_1^2)}{2(1+\rho^2)m_1^2 - m_2} \\ l_\infty = l_0 + \dfrac{m_2 m_1}{2m_1^2(1+\rho^2) - m_2} \end{cases}$$

where ρ is the coefficient of variation of $L_\infty - l_0$. Powell noticed that the bias in the estimates of (θ, l_∞) is $O(\rho^2)$ and may be ignored if ρ^2 is small. Then, approximately

$$(7)\quad \begin{cases} \theta = \dfrac{2m_2 - m_1^2}{2m_1^2 - m_2} \\ l_\infty = l_0 + \dfrac{m_1 m_2}{2m_1^2 - m_2} \end{cases}$$

and θ and l_∞ can be estimated by replacing the true moments on the right-hand side with the moments of the observed length distribution.

The third-moment method

In some cases, the individual variability in growth may be substantial and the $O(\rho^2)$ term cannot be assumed to be zero. Furthermore, it is useful to obtain an estimate of ρ^2 and hence of the variance of L_∞. We can do this by making use of the third moment and assuming a distributional form for L_∞. If $L_\infty - l_0$ is lognormally distributed, then:

$$(8)\quad \begin{cases} \theta = \sqrt{\dfrac{1}{1-\tau}} - 2 \\ l_\infty = l_0 + \left(\sqrt{\dfrac{1}{1-\tau}} - 1\right) m_1 \\ \rho^2 = \dfrac{m_2}{2m_1^2(1-\sqrt{1-\tau})} - 1 \end{cases}$$

where $\tau = 3m_2^3/4m_3m_1^3$. These equations are derived by expressing the moments in terms of the parameters, θ, l_∞, and ρ^2, and solving for them. The moments are given by eq. 5 and Table 1.

Note that distributions other than the lognormal may be used for L_∞. Appendix 2 provides details for three alternative distributional assumptions. The lognormal version will be used in the simulation study.

Simulation studies

It is well known that estimates by the moment method are consistent when the model is correctly specified. Therefore, Powell's method and the regression method give consistent estimates only when there is no individual variability, whereas the third-moment method should provide consistent estimates when the underlying distribution is correctly specified.

We now evaluate the three estimation methods by applying them all to simulated length-frequency data. Since these methods assume constant recruitment, we shall limit our study to the constant recruitment case to focus on the effect of individual variability.

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Fig. 2. (A) Estimates of $\theta = z/k$ (top) and L_∞ (bottom) from 100 simulations of length-frequency data using the three estimation methods. In each simulation, 1000 individuals were generated according to constant recruitment at 20 mm, constant mortality z (with $\theta = 0.5$), and L_∞ randomly sampled from a lognormal distribution with mean 40 mm, lower cut-off 20 mm, and squared coefficient of variation of L_∞ ranging from 0 to 0.13. The distribution of estimates is displayed as box-and-whisker plots, which show the median, interquartile range, and approximate 5th and 95th percentiles. The theoretical estimates obtained from the density function are overlaid as a solid line. (B) As in Fig. 2A, but with $\theta = 2$.

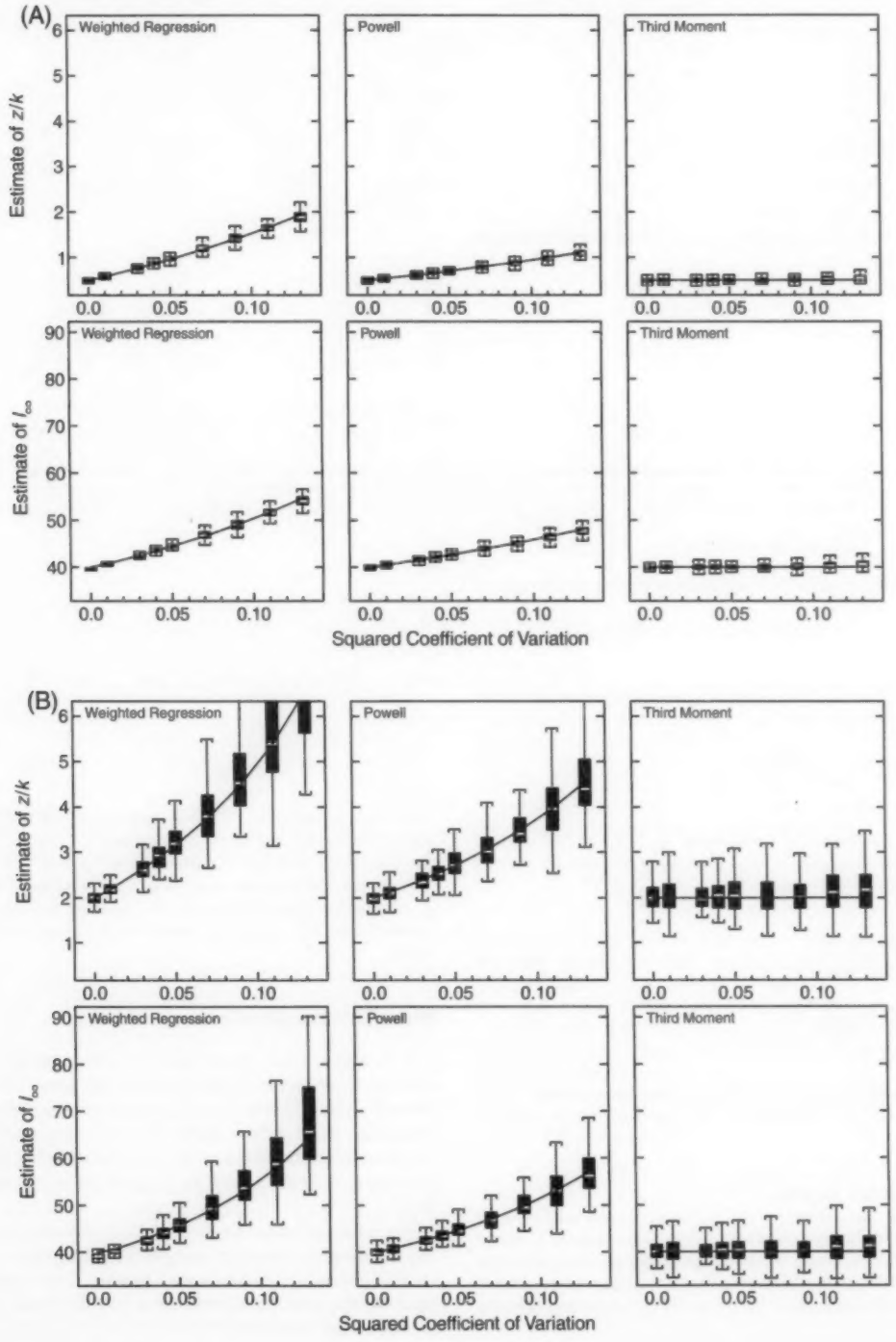

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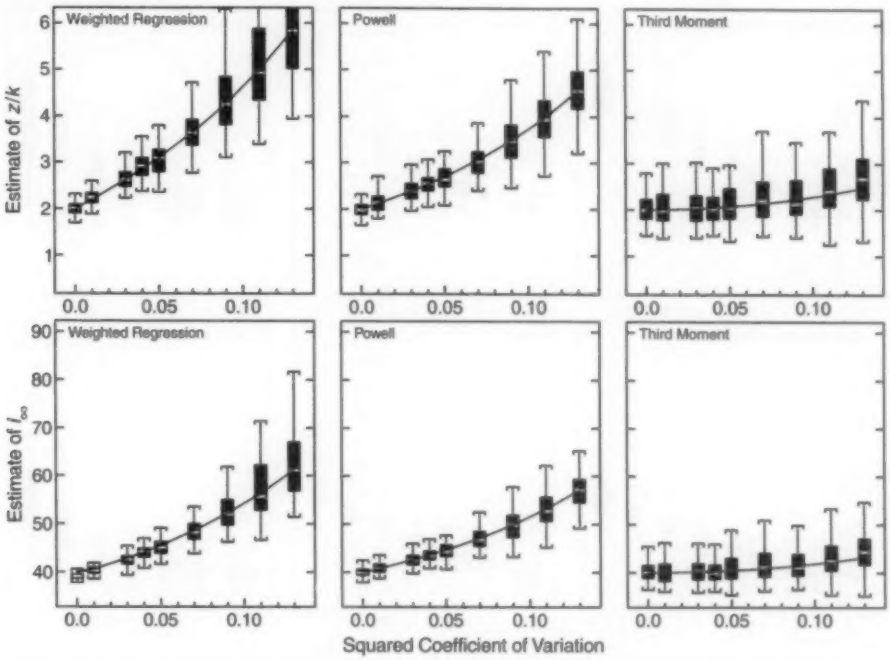
Fig. 3. Estimates of $\theta = z/k$ (top) and l_∞ (bottom) when the underlying L_∞ distribution is gamma, whereas the third-moment method erroneously assumes an underlying lognormal distribution. The 100 simulated length-frequency data sets of 1000 individuals were generated according to constant recruitment at 20 mm, constant mortality z (with $\theta = 2$), and $l_\infty = 40$ mm. The theoretical estimates obtained from the density function are overlaid as a solid line.



We model the individual variability by assuming $L_\infty - l_0$ is lognormally distributed for a range of values of the coefficient of variation. We simulate length-frequency data by sampling from the theoretical length distribution that is derived from the L_∞ distribution. We then generate estimates from the simulated data set for each method. The sampling is repeated 100 times to give a reasonable estimate of the sampling variation in $\hat{\theta}$ and $\hat{l}_\infty$.

We can also find the asymptotic value of the estimates when the sample size is infinite and the length distribution is known without error. This asymptotic value is found by computing the estimate directly from the theoretical length distribution.

We then test the robustness of the lognormal distributional assumption by repeating the simulation for data sampled from different underlying distributions. In this case all three methods are biased. We consider two alternative cases for the distribution of L_∞: the gamma distribution and the truncated normal.

We also carry out a test of the robustness of the assumption of fixed k by repeating a subset of the simulation for data sampled with additional variation in k.

All the simulation work reported here was implemented in S-plus; the code is available via anonymous ftp at ftp://bne.marine.csiro.au/pub/wan032/f9515/zk.

Comparison of methods

We now aim to predict the distribution of real-data estimates by simulation. We follow Powell's example by considering the values $\theta = 0.5$, 1, 2, and 3. We assume $\log(L_\infty - l_0) \sim N(\mu, \sigma^2)$. The parameter σ is approximately the coefficient of variation ρ. We consider values of ρ ranging from 0 to about 36% (which we believe to be a reasonable range for our prawn fishery). Given ρ, we choose μ so that $E(L_\infty) \equiv l_\infty = 40$ mm. The length of recruits, l_0, is 20 mm and recruitment is assumed to be uniform. (The actual choice of units is based on carapace lengths typical for tiger shrimp.)

For each θ and ρ we sample 1000 times from the distribution $f(l)$. This is actually implemented as a sampling from the L_∞ distribution, $p(\cdot)$, followed by a sampling from the age distribution conditional on L_∞ and L_0 given by eq. A3. The sampled lengths are then grouped into 1-mm length classes starting at 20 mm. We then apply each of the three estimation methods to the resulting length-frequency data set. We repeat the procedure 100 times for each θ and ρ.

The asymptotic (infinite sample) estimates for each method are derived from the length density function $f(l)$, which is computed from eq. 4 by numerical integration using a fourth-order scheme. The summation is carried out over a grid that is uniform with respect to the quantiles of the lognormal distribution, except in the neighborhood of the lower limit of the integral; here the integration scheme is modified to handle the integrable singularity in the cases when $0 < \theta < 1$.

The regression method works by regressing $\bar{L}$ on L_m. We adopt a weighted regression scheme with weights equal to the proportion of the population exceeding the truncation length. In practice, regression may be done by inspecting the graph of $\bar{L}$ versus L_m and rejecting points that look out of place beyond some cut-off L_m. Rejection is usually justified

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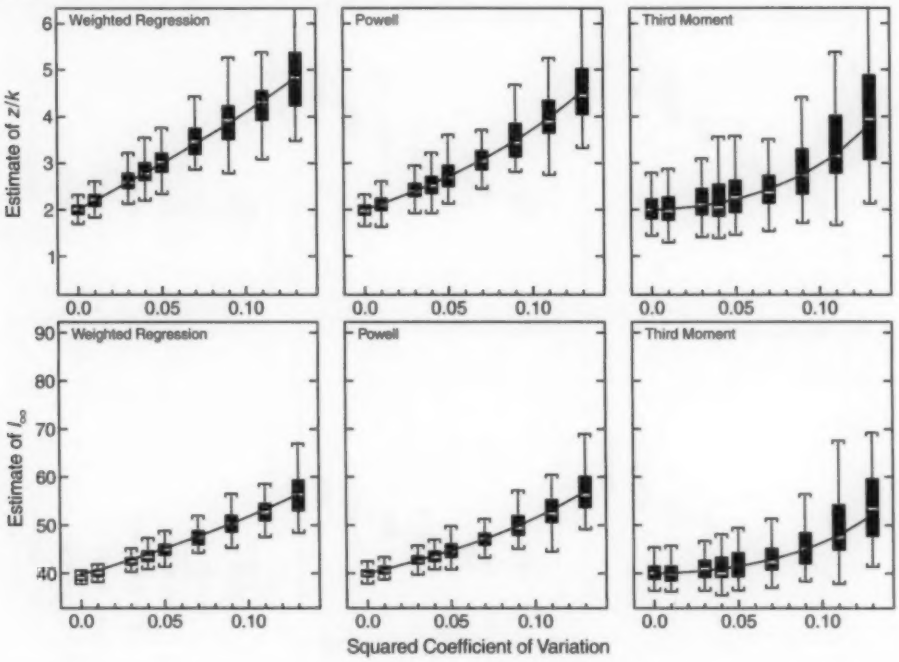
Fig. 4. Estimates of $\theta = z/k$ (top) and l_∞ (bottom) when the underlying L_∞ distribution is truncated normal, whereas the third-moment method erroneously assumes an underlying lognormal distribution. The 100 simulated length-frequency data sets of 1000 individuals were generated according to constant recruitment at 20 mm, constant mortality z (with $\theta = 2$), and $l_\infty = 40$ mm. The theoretical estimates obtained from the density function are overlaid as a solid line.



on the basis of the violation of some assumption (e.g., uniform vulnerability). However, in our simulation, all the basic assumptions are satisfied, so there is no need to resort to ad hoc inspection of graphs, which, in any case, would be difficult to implement.

The results of the simulations for $\theta = 0.5$ and 2 are shown (Fig. 2). Each graph shows box plots of the estimates over the range of ρ^2 values for a particular estimation method. The median, interquartile range, and approximate 5th and 95th percentiles of the 100 estimates are represented in the box plots as a central line, a box and whiskers respectively. A curve showing the asymptotic estimates is overlaid on each graph. For ease of comparison, estimates are plotted on the same scale for all three methods and both values of θ. It is reassuring to see that the asymptotic curves agree well with the means of the box plots. This indicates that the accuracy of the numerical calculation of asymptotic bias and the number of simulations (100) for the box plots are adequate.

With simulated or real data we may sometimes find $\tau > 1$ (see eq. 8) in which case the third-moment estimates become imaginary. This is a potentially serious drawback to the method. However, in our simulations it is a rare occurrence. We found $\tau > 1$ occurred only for the case $\theta = 3$ (not shown) and $\rho^2 \geq 0.09$, and the incidence rate was 6 times in 300 simulations.

It is evident that the weighted regression and Powell methods display positive bias that increases with ρ and θ. Indeed, as Powell said, the bias in his method is almost linear in ρ^2. However, the $O(\rho^2)$ term that has been omitted in eq. 7 is not negligible even for small ρ. The variation of the estimates also increases with both ρ and θ. The third-moment method, on the other hand, is unbiased for all ρ and θ. As for the variance of the estimates, there is a small increase with ρ and a much more substantial increase with θ. For all methods, the variation can be reduced by increasing the sample size. Note that for $\rho = 0$ (when all methods are unbiased) the third-moment method is the most variable. This is because, as one referee pointed out, the third-moment estimates depend more sensitively on the tails of the length distributions, for which there are fewer observations.

Robustness of the distributional assumption

The third-moment method depends on the lognormal distributional assumption. We test the robustness of the third-moment method by applying the methods to simulated data generated from the lognormal distribution and two other distributions: the truncated normal and the gamma. For the distributions to be comparable, we constrain them to have the same mean and coefficient of variation. Note that eq. 5 therefore implies that the three length distributions under comparison are identical in their first two moments. Properties of the distributions are summarized in Appendix 2. In particular, this Appendix shows how we can obtain the parameters of the distribution if we know the mean and coefficient of variation.

For small ρ^2 the length-density functions arising from the three distributions are fairly similar (Fig. 1). For larger ρ^2

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Table 2. Mean and standard deviations (in parentheses) of θ and l_∞ from each of the three methods under comparison for different values of the true parameters θ, ρ (here referred to as ρ_{L_∞}), and ρ_k.

θ	ρ_{L_∞} (%)	ρ_k(%)	Weighted regression	Powell	Third moment
Estimate of θ					
0.5	10	0	0.59 (0.033)	0.54 (0.038)	0.50 (0.050)
		10	0.59 (0.031)	0.54 (0.036)	0.51 (0.049)
		20	0.61 (0.030)	0.56 (0.038)	0.53 (0.051)
	20	0	0.88 (0.051)	0.66 (0.045)	0.51 (0.055)
		10	0.87 (0.056)	0.66 (0.043)	0.51 (0.047)
		20	0.90 (0.053)	0.69 (0.044)	0.53 (0.050)
2.0	10	0	2.20 (0.156)	2.11 (0.194)	2.06 (0.429)
		10	2.24 (0.168)	2.15 (0.206)	2.07 (0.377)
		20	2.34 (0.186)	2.27 (0.204)	2.23 (0.424)
	20	0	2.94 (0.299)	2.56 (0.231)	2.06 (0.341)
		10	2.94 (0.298)	2.59 (0.274)	2.12 (0.428)
		20	3.10 (0.320)	2.77 (0.303)	2.34 (0.563)
Estimate of l_∞					
0.5	10	0	40.65 (0.21)	40.51 (0.29)	40.02 (0.49)
		10	40.64 (0.21)	40.54 (0.30)	40.11 (0.51)
		20	40.68 (0.20)	40.59 (0.30)	40.15 (0.51)
	20	0	43.57 (0.46)	42.18 (0.45)	40.07 (0.61)
		10	43.47 (0.51)	42.11 (0.43)	40.04 (0.51)
		20	43.61 (0.50)	42.26 (0.46)	40.17 (0.57)
2.0	10	0	40.17 (0.76)	40.80 (1.09)	40.44 (2.70)
		10	40.34 (0.85)	40.95 (1.18)	40.42 (2.35)
		20	40.80 (0.93)	41.57 (1.16)	41.36 (2.66)
	20	0	44.30 (1.64)	43.71 (1.43)	40.39 (2.18)
		10	44.30 (1.63)	43.83 (1.64)	40.72 (2.69)
		20	45.18 (1.63)	44.91 (1.73)	42.04 (3.54)

Note: The underlying distribution of L_∞ is lognormal and l_∞ = 40 mm. The case ρ_k = 0% is the case of fixed k, which corresponds to the data in Figs. 2A and 2B with ρ^2 = 0.01 and 0.04.

the three densities take on their own character, with the lognormal and gamma densities resembling each other more closely than the truncated normal.

Simulation results using data generated from the underlying gamma distribution have been obtained, again for θ = 0.5 and 2. We show the results for θ = 2 in Fig. 3, where the same scale has been used as in Fig. 2. The results are very similar to the results for the lognormal distribution. There is a small positive bias for the third-moment method, which increases with ρ and θ. However, this bias is much less than that for Powell's method or the regression method.

The results for an underlying truncated normal distribution are shown in Fig. 4. Curiously, the weighted regression estimates have improved. The bias in the third-moment method is now larger still because the truncated normal distribution is even more different from the lognormal than the gamma distribution. The third-moment method is still less biased than Powell's method for θ = 0.5. However, for θ = 2 the improvement becomes less clear-cut for $\rho^2 > 0.10$ (ρ > 32%).

Robustness of the fixed-k assumption

We have assumed that the parameter k is the same for all individuals. We test this assumption by allowing k to be a lognormal random variable. As in the previous robustness study, we have run all the estimation methods on simulated data generated under the additional property of random k. This means that, for each simulation, we have taken 1000 samples from the k distribution, independently of the samples for L_∞ and age. We let k have a mean of 3·year^{-1}, and we allow two levels (10 and 20%) for the coefficient of variation ρ_k. We consider two cases for the mortality (z = 1.5 and 6) corresponding to θ = 0.5 and 2, where now θ = z/E(k). The underlying L_∞ distribution is lognormal with two levels of variation: ρ_{L_∞} = 10 and 20% (the subscript L_∞ is added to avoid confusion with ρ_k). The simulations of the comparison study provide control cases corresponding to ρ_k = 0%.

The means and standard deviations of the estimates of θ and l_∞ over 100 simulations are shown in Table 2. The effect of variable k is to add a positive bias to all the estimates. The size of the extra bias increases with ρ_k, ρ_{L_∞}, and θ and is approximately independent of the method. The bias in the third-moment method caused by random k is the same order of magnitude as the bias due to the truncated normal distribution.

Discussion

The Beverton–Holt equation (eq. 2) was originally derived under the assumption of constant L_∞. Later, Powell noticed that the equation still holds when L_∞ follows a distribution, provided the lower cutoff, L_m, equals the minimum recruitment length, l_0. The result follows easily from eq. 5 after setting n = 1. We have assumed the cutoff chosen by the experimenter L_m and the minimum length of the re-

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cruited population l_0 are the same, thus avoiding more complicated conditional moment formulas. However, for $L_m > l_0$, eq. 2 is no longer valid because the length distribution must be replaced by a truncated distribution. In general, the truncated nth moment relative to L_m is given by

$$(9) \qquad m_n = \mathrm{E}\{(L - L_m)^n \mid L \geq L_m\} = \frac{\int_{L_m}^{\infty} (l - L_m)^n f(l)\,\mathrm{d}l}{\int_{L_m}^{\infty} f(l)\,\mathrm{d}l}$$

The numerator of the right-hand side of this equation becomes

$$(10) \qquad \mathrm{E}\{(L - L_m)^n I(L \geq L_m)\} = \frac{\Gamma(n+1)\Gamma(\theta+1)}{\Gamma(n+\theta+1)} \mathrm{E}\left\{\frac{(L_\infty - L_m)^{n+\theta}}{(L_\infty - l_0)^\theta} I(L_\infty \geq L_m)\right\}$$

where $I(\cdot)$ is an indicator function. The denominator is given by the same expression with $n = 0$. Therefore, the truncated moments of the length distribution are no longer simply proportional to the moments of the L_∞ distribution; instead, a weighting term $((L_\infty - L_m)/(L_\infty - l_0))^\theta$ must be introduced. This weighting term has the effect of increasing the overall slope of $\bar{L}$ against L_m, thus leading to an overestimate of β and so of θ.

In this paper we have used the methods on a very idealized case, namely uniform recruitment at constant length and constant mortality, an assumption that is unlikely to be true in practice. It is also probably true that both k and L_∞ may vary between individuals. However, as pointed out by Wang et al. (1995), it is generally adequate to allow L_∞ to vary to account for individual variability. The simplified models investigated here allow us to see more clearly the effect of individual variability. It would serve little purpose to compare the methods on a more complicated model with, say, seasonal recruitment and effort because the inaccuracy in the methods would be due to several causes.

The simulation studies show that all methods are biased when distributional assumptions are violated. The third-moment method, although performing better in terms of bias, is not wholly satisfactory. Other modifications to Beverton and Holt's method (Ssentongo and Larkin 1973; Ebert 1980; Hoenig 1987) have strong limitations and disadvantages, as pointed out by Vetter (1988). Therefore, we believe there is a need to develop more comprehensive models to accommodate general aspects. We have developed a maximum-likelihood approach incorporating individual variability and arbitrary recruitment pattern and time-varying mortality (Y.-G. Wang and N. Ellis, unpublished).

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References

Beverton, R.J.H., and Holt, S.J. 1956. A review of methods for estimating mortality rates of fish in exploited fish populations, with special reference to sources of bias in catch sampling. Rapp. P.V. Reun. Cons. Int. Explor. Mer, **140**: 67–83.

Ebert, T.A. 1980. Estimating mortality from growth parameters and a size distribution when recruitment is periodic. Limnol. Oceanogr. **26**: 764–769.

Hoenig, J.M. 1987. Estimation of growth and mortality parameters for use in length-structure stock production models. *In* Length-based methods in fisheries research. *Edited by* D. Pauly and G.R. Morgan. ICLARM Conf. Proc. No. 13. International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait. pp. 121–128.

Powell, D.G. 1979. Estimation of mortality and growth parameters from the length frequency of a catch. Rapp. P.V. Reun. Cons. Int. Explor. Mer, **175**: 167–169.

Sainsbury, K.J. 1980. Effect of individual variability on the von Bertalanffy growth equation. Can. J. Fish. Aquat. Sci. **37**: 241–247.

Ssentongo, G.W., and Larkin, P.A. 1973. Some simple methods of estimating mortality rates of exploited fish populations. J. Fish. Res. Board. Can. **30**: 695–698.

Vetter, E.F. 1988. Estimation of natural mortality in fish stocks: a review. Fish. Bull. U.S. **86**: 25–43.

Wang, Y.G., Thomas, M.R., and Somers, I.F. 1995. A maximum likelihood approach for estimating growth parameters from tag–recapture data. Can. J. Fish. Aquat. Sci. **52**: 252–259.

Wetherall, J.A., Polovina, J.J., and Ralston, S. 1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data. *In* Length-based methods in fisheries research. ICLARM Conf. Proc. No. 13. *Edited by* D. Pauly and G.R. Morgan. International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait. pp. 53–75.

Appendix 1. Derivation of eq. 4

If $f(l)$ is the probability density function of L, then

$$(A1) \qquad f(l) = \int_l^{\infty} p(x) f(l \mid L_\infty = x)\,\mathrm{d}x$$

where $f(l|L_\infty = x)$ is the probability density function of L when L_∞ is known to equal x.

If L_∞ is known the the random variables L, age A and age at recruitment A_0 are deterministically linked by eq. 1. Therefore $f(l|L_\infty = x)$ can be expressed in terms of the conditional age density function, $h(a|L_\infty = x, A_0 = a_0)$, as

$$(A2) \qquad f(l \mid L_\infty = x) = \frac{1}{k(x-l)} h(-k^{-1} \log(1 - l/x) \mid x)$$

The age distribution satisfies

$$h(a \mid L_\infty = x, A_0 = a_0) = z\mathrm{e}^{-(a-a_0)z}$$

We therefore have

$$(A3) \qquad h(a \mid L_\infty = x) = h(a \mid L_\infty = x, A_0 = -k^{-1} \log(1 - l_0/-x)) = z\left(\frac{x}{x - l_0}\right)^\theta \mathrm{e}^{-az}$$

and eq. 4 follows from eqs. A1, A2, and A3.

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Appendix 2. Third-moment estimation under various distributional assumptions

The form of the third-moment estimators depends on the assumed distribution of L_∞. Table 1 gives properties of the lognormal distribution and the two other distributions that were used in the robustness study. The table shows how the two parameters of each distribution can be computed from the mean and coefficient of variation (note that $\mu_1 = l_\infty - l_0$). Also shown are the moments, μ_i, of the distribution in terms of its parameters.

The truncated normal case requires further explanation. The parameter x_0 is found by solving the equation for ρ^2: the solution x_0 is the limit of the sequence u_i ($i = 0, 1,...$), where

$$u_0 = 0$$

and

$$u_{i+1} = \frac{2(\psi(u_i)^2(1+\rho^2) - 1)}{\psi(u_i)(1+2\rho^2) + \sqrt{\psi(u_i)^2 + 4\rho^2}}$$

We will use $\phi(\cdot)$ to denote the standard normal probability density function and $\Phi_c(\cdot)$ to denote the standard normal complementary cumulative density function. For convenience, we define $\psi(x) = \phi(x)/\Phi_c(x)$, $G(x) = \psi(x) - x$, $x_0 = (l_0 - \mu)/\sigma$, and $G_0 = G(x_0)$. Note that $\mu_i = E((L_\infty - l_0)^i)$ and $m_i = E((L - l_0)^i)$, which are the moments of the L_∞ and L distributions, respectively. Therefore, μ_i can be defined by the following recurrence relation:

$$\text{(A4)} \quad \mu_n = (n-1)\sigma^2\mu_{n-2} - x_0\sigma\mu_{n-1}$$

with $\mu_0 = 1$ and $\mu_1 = \sigma G_0$.

The moments of the length distribution m_i depend on $p(\cdot)$ only through its moments μ_i, thus

$$m_i = \frac{\Gamma(i+1)\Gamma(\theta+1)\mu_i}{\Gamma(\theta+i+1)}$$

This is a restatement of eq. 5.

The lower section of Table 1 shows the estimates of ρ^2, θ, and l_∞ in terms of quantities derived from the first three moment estimates. The estimate of the auxiliary parameter, x_0, namely $\hat{x}_0$, is the solution of the equation

$$\text{(A5)} \quad M_3G(x)((x^2+2)G(x) - x) + M_2G(x)^2(1 - xG(x)) - 4(1 - xG(x))^2 = 0$$

Being a nonlinear equation in a single variable, this equation can easily be solved numerically, provided a root exists. We suspect, however, that it is possible to obtain data that leave this equation with no real solution.

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Declines in benthic macroinvertebrate populations in southern Lake Michigan, 1980–1993

Thomas F. Nalepa, David J. Hartson, David L. Fanslow, Gregory A. Lang, and Stephen J. Lozano

Abstract: Densities of the major benthic macroinvertebrate groups declined dramatically at sites shallower than 50 m in southern Lake Michigan between 1980 and 1993. Declines in *Diporeia*, Oligochaeta, and Sphaeriidae ranged from 40 to 75% at these depths. Total densities declined from 16 800·m^{-2} in 1980–1981 to 4800·m^{-2} in 1992–1993 at sites in the 16–30 m depth interval and from 21 300 to 11 300·m^{-2} at sites in the 31–50 m depth interval. Changes at sites deeper than 50 m were minimal; only sphaeriids declined to any extent. Declines in oligochaetes and sphaeriids occurred uniformly throughout the nearshore region and over the entire sampling period. Declines in these two groups were most likely related to reductions in phosphorus loads and a general decrease in productivity in the nearshore area over the sampling period. On the other hand, declines in *Diporeia* occurred mainly in the later portion of the sampling period and were greatest in the southeastern region of the lake. Densities at many sites in the southeastern region were <100·m^{-2} in 1993, down from 3000–8000·m^{-2} in 1980–1987. We hypothesize that the filtering activities of large populations of *Dreissena polymorpha* in nearshore waters may be having a negative impact on *Diporeia* in deeper waters by decreasing the amount of food available to this surface-feeding detritivore.

Résumé : La densité des principaux groupes de macroinvertébrés benthiques a fortement diminué entre 1980 et 1993 dans les zones peu profondes (<50 m) du sud du lac Michigan. Les déclins observés chez *Diporeia*, les oligochètes et les sphaeriides atteignaient 40 à 75% à ces profondeurs. Les densités totales sont passées de 16 800·m^{-2} en 1980–1981 à 4 800·m^{-2} en 1992–1993 dans les zones de 16 à 30 m de profondeur et de 21 300 à 11 300·m^{-2} dans les zones de 31 à 50 m de profondeur. Dans les secteurs plus profonds, les changements étaient de façon générale peu importants, les seuls déclins prononcés ayant été observés chez les sphaeriides. Les déclins chez les oligochètes et les sphaeriides se sont produits de façon uniforme à l'échelle de toute la zone côtière et durant toute la durée de l'échantillonnage. Les déclins chez ces deux groupes étaient vraisemblablement attribuables à des réductions des charges de phosphore et à une diminution générale de la productivité dans la zone côtière durant la période d'échantillonnage. Chez *Diporeia*, les déclins ont été observés principalement durant la dernière portion de la période d'échantillonnage et se sont révélés plus prononcés dans la région sud-est du lac. En plusieurs endroits de cette région, les densités sont passées de 3 000 à 8 000·m^{-2} en 1980–1987 à <100·m^{-2} en 1993. Nous croyons que la filtration exercée par les fortes populations de *Dreissena polymorpha* dans les eaux côtières pourrait avoir nui aux populations de *Diporeia* établies en zones plus profondes en réduisant la quantité de nourriture disponible pour cette espèce détritivore se nourrissant en surface.

[Traduit par la Rédaction]

Introduction

Over the past few decades, nearshore regions of the Great Lakes have undergone dramatic changes in real and perceived trophic status as a result of two important events: the planned reduction of nutrient loads and the establishment of the zebra mussel (*Dreissena polymorpha*). Reductions in phosphorus inputs have led to declines in phytoplankton abundances and shifts in algal species composition in nearshore waters (Edsall and Charlton 1996) whereas the filtering activities of *D. polymorpha* have reduced phytoplankton, increased water clarity, and shifted productivity from the pelagic to the benthic region without any real change in trophic status (Fahnenstiel et al. 1995*a*, 1995*b*). Because benthic macroinvertebrate communities integrate changes in both the pelagic and benthic regions, trends in abundances and species composition are useful in assessing changes in overall system productivity as well as interpreting causes of observed changes.

Prior to the mid-1970s, excessive nutrient loads (phosphorus) in the Great Lakes led to increased pelagic productivity and deterioration of the benthic environment. Macroinvertebrate species that could best take advantage of increased

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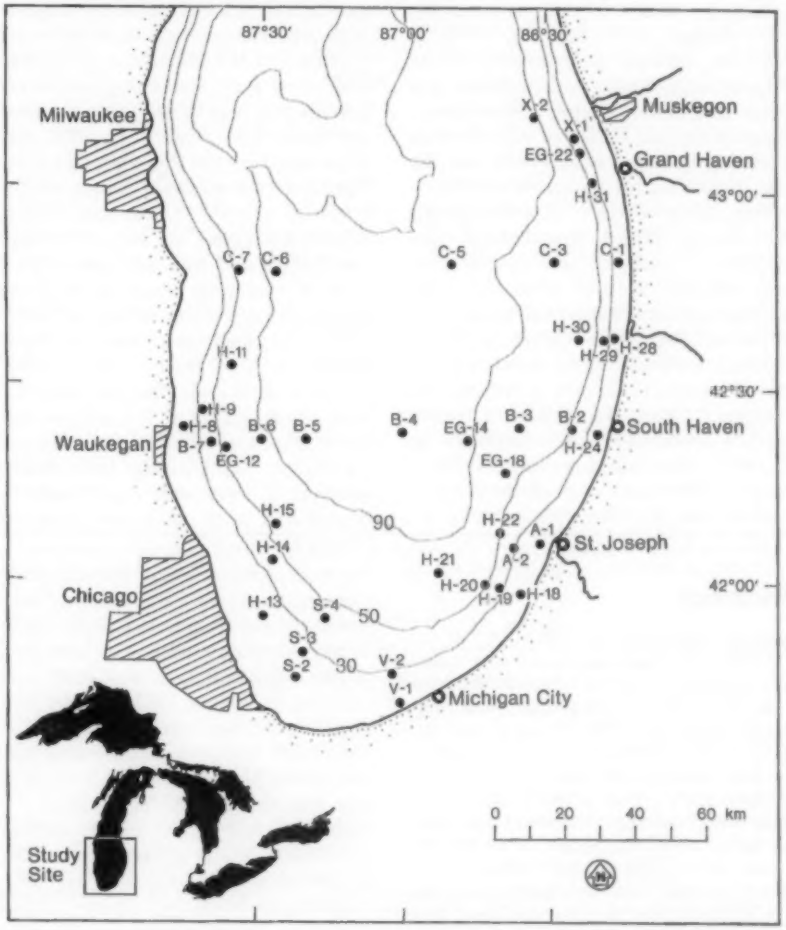
Fig. 1. Location of the 40 sampling sites in southern Lake Michigan. Depth contours of 30, 50, and 90 m define the depth intervals by which the stations were grouped for data analysis. Each station represents a site that was originally sampled in the 1960s or earlier. Derivation of site designations is described in Nalepa (1987).



food inputs to the benthic region became abundant, while more sensitive forms declined (see Cook and Johnson 1974 for review). Since the reduction of phosphorus loads, there has been a general shift to communities indicative of improved conditions; changes in densities and species composition have generally been the reverse of changes when conditions were deteriorating (Johnson and McNeil 1986; Schloesser et al. 1995). For instance, in the Bay of Quinte, the density and biomass of some major benthic groups (oligochaetes, sphaeriids, and chironomids) declined between 1966 and 1984 in response to a decline in phosphorus loads and bay productivity (Johnson and McNeil 1986). Also, in western Lake Erie, declines in oligochaete abundances and shifts in species composition in nearshore waters between 1961 and 1982 indicated improved water quality (Schloesser et al. 1995).

The introduction and widespread abundance of *D. polymorpha* have confounded our interpretations of trophic trends using benthic macroinvertebrate communities. The overall impact of *D. polymorpha*'s filtering activities on benthic populations has varied, depending on the feeding mode and life habit of the particular species or taxonomic group. *Dreissena polymorpha* has had a negative impact on some taxa via competitive exclusion (Nalepa et al. 1996; Dermott and Kerec 1997), a positive impact by increasing habitat complexity and detrital food (Stewart and Haynes 1994, Botts et al. 1996), or no impact at all (Dermott and Kerec 1997).

In this study, we assess long-term changes in benthic macroinvertebrate populations of the southern basin of Lake Michigan. Benthic communities in this basin are greatly influenced by changes in nutrient loads, since a large portion (43%) of suspended material and total phosphorus enters the lake at the southern end (Robertson 1997). We collected samples in 1986–1987 and in 1992–1993 at the same sites that were sampled in 1980–1981 (Nalepa 1987). In the 1980–1981 survey, densities of the major benthic macroinvertebrate groups (*Diporeia* (Amphipoda), Oligochaeta, and Sphaeriidae) increased over twofold between the mid-1960s and 1980–1981 at depths <50 m (Nalepa 1987). This finding

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followed a similar trend of increasing densities between the early 1930s and 1964 (Robertson and Alley 1966). Both studies attributed increased densities to accelerated nutrient loads and higher productivity within the lake between the 1950s and early 1970s (Chapra 1977; Schelske 1978). A positive, direct relationship between pelagic productivity and densities of amphipods, oligochaetes, and sphaeriids is a common feature of large, deep lakes (Saether 1980). Reductions in phosphorus loads in the mid-1970s led to declines in total phosphorus, summer epilimnetic chlorophyll, and the intensity of the spring diatom bloom by the late 1970s – early 1980s (Vandercastle 1985; Scavia et al. 1986; Chang and Rossman 1988). Nalepa (1987) hypothesized that macroinvertebrate densities in southern Lake Michigan in 1980–1981 had not yet reflected observed productivity declines in the pelagic region. Since phosphorus loads have continued to decline through the 1980s (Johengen et al. 1994), our subsequent surveys were designed to determine if the macroinvertebrate community had now responded to these productivity changes. Furthermore, with *D. polymorpha* becoming established in southern Lake Michigan in 1989 (Marsden et al. 1993), our surveys provide a relative measure of initial changes in the macroinvertebrate community that may have resulted from *D. polymorpha* filtering activities.

Materials and methods

Samples were collected in 1986–1987 and 1992–1993 at the same 40 sites sampled in 1980–1981 using exactly the same methods (Nalepa 1987) (Fig. 1). Bottom substrates ranged from coarse sand and gravel to fine silt, and sampling depths ranged from 16 to 157 m. Exact location, water depth, and substrate type at each site are given in Nalepa et al. (1985). Sampling was conducted in spring (mid-May – early June), summer (late July – early August), and fall (September–October) over a 1-week period in each season of each year. The sampling period sometimes extended longer than 1 week because of poor weather conditions. Samples were taken in triplicate with a Ponar grab (area = 0.046 m^2) and washed into an elutriation device fitted with a nitex sleeve having 0.5-mm openings (Nalepa et al. 1985). Retained material was immediately preserved in 10% buffered formalin containing rose bengal stain.

Retained residue was placed into a white enamel pan and organisms were picked, counted, and sorted into major benthic groups (*Diporeia*, Oligochaeta, Sphaeriidae, Chironomidae, Gastropoda, *D. polymorpha*, and others). In some samples, the number of organisms was extremely large and only a randomly chosen portion (one eighth to one half) of the residue was picked and then applied to the entire sample. All organisms collected in 1980–1981 and 1992–1993 were identified to the lowest practical taxonomic level, but organisms collected in 1986–1987 were identified only to the group level as given above. For oligochaetes, between 75 and 100 individuals in a replicate (proportionately split with a Folsom plankton splitter when numbers were higher) were cleared in lactophenol before identification. Only oligochaetes with a prostomium were included in abundance estimates. Since fragments (without prostomium) can only be recognized during the process of species identification and not when counted and sorted, the total number of oligochaetes in 1986–1987 at each site was corrected based on the mean proportion of fragments found in the other four years at the same site.

Results

Spatial and temporal trends were examined by dividing the sampling sites into four depth intervals (16–30, 31–50, 51–90, and >90 m) and calculating yearly means for the three major macroinvertebrate groups, *Diporeia*, Oligochaeta, and Sphaeriidae. These depth intervals are consistent with prior characterization of depth–macroinvertebrate associations in Lake Michigan (Alley and Mozley 1975; Nalepa 1987) and approximate regions of varying sediment resuspension and deposition within the southern basin (Chambers and Eadie 1981; Eadie et al. 1984). Between 1980 and 1993, there was a general downward trend in density in each of the three macroinvertebrate groups at the 16–30 and 31–50 m intervals (Table 1). At these two shallowest intervals, *Diporeia* declined 68 and 43%, respectively, oligochaetes declined 75 and 40%, and sphaeriids declined 75 and 72%. Overall, total mean density at the 11 sites in the 16–30 m interval declined from 16 800·m^{-2} in 1980 to 4800·m^{-2} in 1993, while total mean density at the 12 sites in the 31–50 m interval declined from 21 300 to 11 300·m^{-2}. Yearly differences at these two shallow intervals were significant for each group (ANOVA, $P < 0.01$) except for sphaeriids at 16–30 m ($P = 0.16$) (Table 1). When yearly differences were significant, multiple range tests (Tukey HSD) indicated that densities in 1993 were significantly lower ($P < 0.05$) than densities in most other years except for densities in 1992 (Table 1).

Density trends at the two deeper intervals were not as consistent as at the shallower intervals. Overall, a downward trend in total density was not readily apparent (Table 1). Yearly differences were significant for *Diporeia* at these two deeper depth intervals ($P < 0.001$), but mean densities of *Diporeia* in 1992 or 1993 were not always lower than means in previous years (see low densities in 1981 at both intervals; Table 1). For oligochaetes, densities at the 51–90 m interval were lowest in 1993, but were only significantly lower than densities in 1980 (Tukey HSD, $P < 0.05$). Yearly differences in density at the >90 m interval were not significant ($P = 0.80$). Yearly differences in sphaereiid densities were significant at both intervals ($P < 0.05$), with lowest densities occurring in 1993.

Since the 1986–1987 survey was conducted just prior to the establishment of *D. polymorpha* in Lake Michigan, these survey years are important when comparing potential impacts of phosphorus reductions versus *D. polymorpha* filtering activities. Declines between 1980–1981 and 1986–1987 represent potential responses to phosphorus load reductions, while declines between 1986–1987 and 1992–1993 represent potential responses to both phosphorus reductions and *D. polymorpha*. In order to distinguish the relative impact of these two events, we calculated and then compared rates of decline (percent decline per year) for the two time periods (1980–1981 to 1986–1987, 1986–1987 to 1992–1993) for each of the three groups (Table 2). At the 16–30 m interval, rates of decline were greater in the 1980–1981 to 1986–1987 time period for oligochaetes and sphaeriids, but greater in the 1986–1987 to 1992–1993 time period for *Diporeia*. Decline rates in oligochaetes were significant for both time periods (paired *t*-test, $P < 0.05$) (Table 2), declines in *Diporeia* were significant only in the later period, and declines in sphaeriids were not significant ($P > 0.05$) for either period. This suggests that, of the three groups, oligochaetes were most responsive to nutrient reductions and that *Diporeia*

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Table 1. Mean (± SE) yearly densities (no.·m^{-2}) of the three major macroinvertebrate groups at various depth intervals in southern Lake Michigan.

	1980	1981	1986	1987	1992	1993	ANOVA
Depth: 16–30 m							
Diporeia	8 310±1242*a*	7 455±987*a*	8 041±1292*a*	5 377±826*a*	2 618±504*b*	2 698±543*b*	<0.001
Oligochaeta	6 393±2286*a*	5 613±1578*a*	3 127±933*ab*	2 925±960*ab*	1 713±376*ab*	1 647±434*b*	0.002
Sphaeriidae	2 129±577	2 643±741	1 257±345	1 348±347	1 381±384	535±123	0.156
Total	16 832	15 711	12 425	9 650	5 712	4 880	
Depth: 31–50 m							
Diporeia	12 216±995*a*	9 693±622*a*	10 377±523*a*	10 524±594*a*	8 710±759*ab*	7 021±870*b*	0.003
Oligochaeta	5 308±410*a*	4 692±349*a*	4 722±463*a*	5 004±584*a*	4 487±466*ab*	3 166±330*b*	0.002
Sphaeriidae	3 789±396*a*	2 862±381*a*	2 394±255*a*	3 083±418*a*	2 273±303*a*	1 068±166*b*	<0.001
Total	21 313	17 247	17 493	18 611	15 470	11 255	
Depth: 51–90 m							
Diporeia	6 466±285*ac*	5 071±375*b*	6 622±456*ac*	7 652±346*ac*	6 380±332*ac*	5 352±373*ab*	<0.001
Oligochaeta	2 190±184*a*	2 077±154*ab*	2 248±204*ab*	1 976±232*ab*	2 042±135*ab*	1 530±97*b*	0.026
Sphaeriidae	758±93*a*	844±98*a*	838±122*a*	797±111*a*	801±153*a*	384±72*b*	<0.001
Total	9 414	7 992	9 708	10 425	9 223	7 266	
Depth: >90 m							
Diporeia	3 662±363*a*	2 407±357*b*	5 314±537*a*	4 672±356*a*	3 195±389*ab*	3 226±515*ab*	<0.001
Oligochaeta	989±167	1 007±227	1 132±271	1 384±426	1 179±151	1 123±159	0.794
Sphaeriidae	198±37*a*	191±53*ab*	329±184*ab*	151±46*ab*	113±30*ab*	98±36*b*	0.028
Total	4 849	3 605	6 775	6 207	4 487	4 447	

Note: Differences between years were tested using ANOVA on log(x + 1)-transformed values. Statistical tests and estimates of variability were based on means of three replicates per site per sampling date. Values followed by a different letter are significantly different (Tukey HSD, $P < 0.05$).

Table 2. Rates of decline for the three major macroinvertebrate groups for each survey period.

	Diporeia	Oligochaeta	Sphaeriidae
Depth: 16–30 m			
1980–1981 to 1986–1987	2.6 (6, 0.345)	8.2 (9, 0.014)	7.5 (7, 0.216)
1986–1987 to 1992–1993	10.0 (8, 0.005)	7.4 (6, 0.009)	4.5 (8, 0.069)
1980–1981 to 1992–1993	5.5 (11, <0.001)	6.0 (11, 0.001)	5.0 (11, 0.006)
Depth: 30–50 m			
1980–1981 to 1986–1987	0.7 (6, 0.758)	0.5 (7, 0.403)	2.9 (7, 0.549)
1986–1987 to 1992–1993	4.1 (8, 0.014)	3.5 (10, 0.002)	6.5 (8, 0.031)
1980–1981 to 1992–1993	2.3 (8, 0.085)	2.0 (11, 0.003)	4.1 (12, 0.001)

Note: Declines were calculated as the percent decline per year (assume 6 years between surveys). The first value in parentheses is the number of sites showing a decrease in densities over the given time period. The second value in parentheses is the P for a paired t-test comparing densities of all sites in that depth interval. For the 16–30 m interval, one site was not collected in 1986–1987; thus, $n = 10$ for the first two time periods and $n = 11$ for the last. Similarly, one site was not sampled in the 31–50 m interval in 1986–1987; thus, $n = 11$ for the first two time periods and $n = 12$ for the last.

may have been most affected by *D. polymorpha*. For the 31–50 m interval, rates of decline in all three groups were greater in the 1986–1987 to 1992–1993 time period. Declines were significant ($P < 0.05$) (Table 2) for each group during this later period, but were not significant for the earlier period ($P > 0.05$).

The effects of sampling season (spring, summer, fall) were not significant for any of the groups (ANOVA, log(x + 1)-transformed, $P > 0.05$) except for *Diporeia* at the 16–30 m interval ($P = 0.02$). *Diporeia* abundances were highest in the spring and declined through summer and fall. This species has a 1-year life cycle at these depths, and population densities are high in the spring when newly hatched young enter the population but then decline (Winnell and White 1984).

Declines in densities were observed at most all sites <50 m between 1980–1981 and 1992–1993 (Table 2). To determine if declines occurred to a similar extent over all sites at these depths, all sites <50 m (23 total) were ranked by relative mean density in both 1980–1981 and 1992–1993 and rank differences between the two 2-year surveys compared. For oligochaetes and sphaeriids, rank differences were not significant (chi-square, $P > 0.05$), indicating that relative declines in these two groups were consistent for all sites at these depths. However, for *Diporeia*, there was a significant difference in ranks ($P < 0.01$), indicating that densities at some sites declined more than at others. Clearly, *Diporeia* declined to a greater extent at sites <50 m in the southeastern portion of the lake (Fig. 2). All 11 sites where *Diporeia* declined more than 60% between 1980–1981 and 1992–1993 were located in this area of the lake (Fig. 3). The mean decline at these sites was 81.6% (range 60.3–99.2%), while the mean decline at the other sites where *Diporeia* decreased was only 26.2% (range 7.0–49.0%). At four of the sites (A-1, H-18, S-2, V-1), densities in 1993 were <100·m^{-2}. Mean densities at these same sites in 1980–1987 ranged from 3381 to 8294·m^{-2}.

The trophic status of the most common oligochaete species is generally well known; thus, community composition

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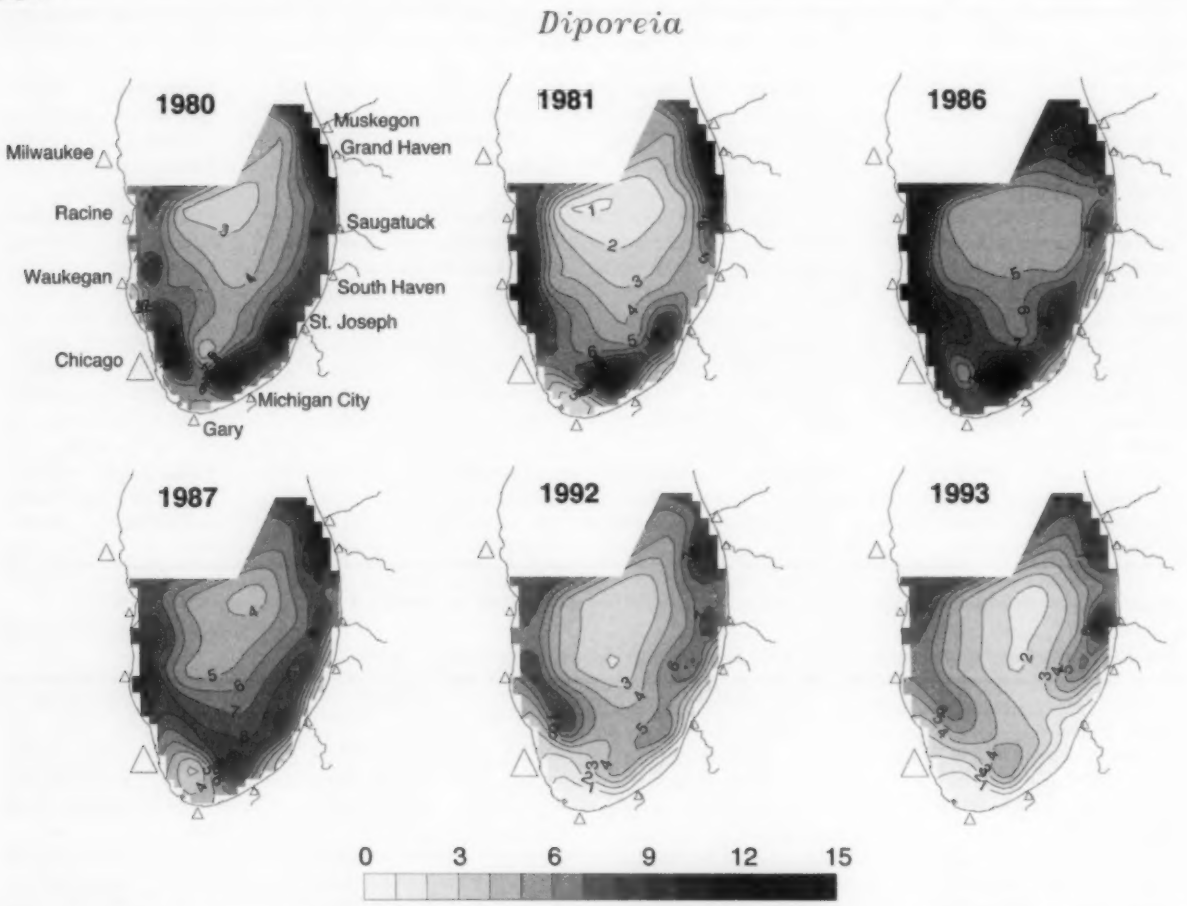
Fig. 2. Densities (no.·m^{-2} × 10^3) of *Diporeia*, Oligochaeta, and Sphaeriidae in each of the survey years. (Figure 2 is continued on next page.)



has often been used to assess a lake's trophic state (Milbrink 1983; Lauritsen et al. 1985) and also to assess changes in trophic state over time (Lang and Reymond 1992; Schloesser et al. 1995). Species can be divided into three categories based on their distribution and abundance relative to known areas of enrichment: type 1, largely restricted to oligotrophic waters; type 2, characteristic of mesotrophic conditions; type 3, tolerant of extreme organic enrichment. The abundance of each of the major species and the percentage of individuals in each trophic category in 1980–1981 and 1992–1993 were compared (Table 3). Dominant species in each category, regardless of time period, were *Stylodrilus heringianus* in type 1 (98%), *Potamothrix vejdovskyi* in type 2 (73%), and *Limnodrilus hoffmeisteri* in type 3 (72%). The proportion of individuals in each trophic category (relative to the total number collected) changed significantly (chi-square, $P < 0.05$) between 1980–1981 and 1992–1993 at each depth interval (Table 3). In effect, differences between the two survey periods were a result of changes in the proportion of type 1 individuals, essentially all *S. heringianus*, and of changes in the proportion of individuals categorized as unidentifiable immatures. The proportion of *S. heringianus* increased between 1980–1981 and 1992–1993 at the 16–30, 51–90, and >90 m intervals, while the proportion of unidentifiable immatures declined. Because *S. heringianus* can be identified to species even when immature, most of the unidentifiable individuals were likely species of types 2 and 3. These changes would indicate less eutrophic conditions in 1992–1993 than in 1980–1981 at these depths. However, changes in species composition at the 31–50 m interval were inconsistent with those at the other three depth intervals. The proportion of *S. heringianus* declined, while the proportion and actual abundance of unidentifiable immatures increased (Table 3).

Other commonly collected macroinvertebrate taxa included Chironomidae, Gastropoda, and *D. polymorpha*. Densities of the former two taxa were low, and they comprised only a minor portion of the total macroinvertebrate community. Mean yearly densities between 1980 and 1993 were highest at the 16–30 m interval for both taxa and ranged from 173 to 320·m^{-2} for chironomids and from 13 to 88·m^{-2} for gastropods. Of special interest are the abundance and distribution of *D. polymorpha*, since the filtering activities of this species can affect food inputs to macroinvertebrate

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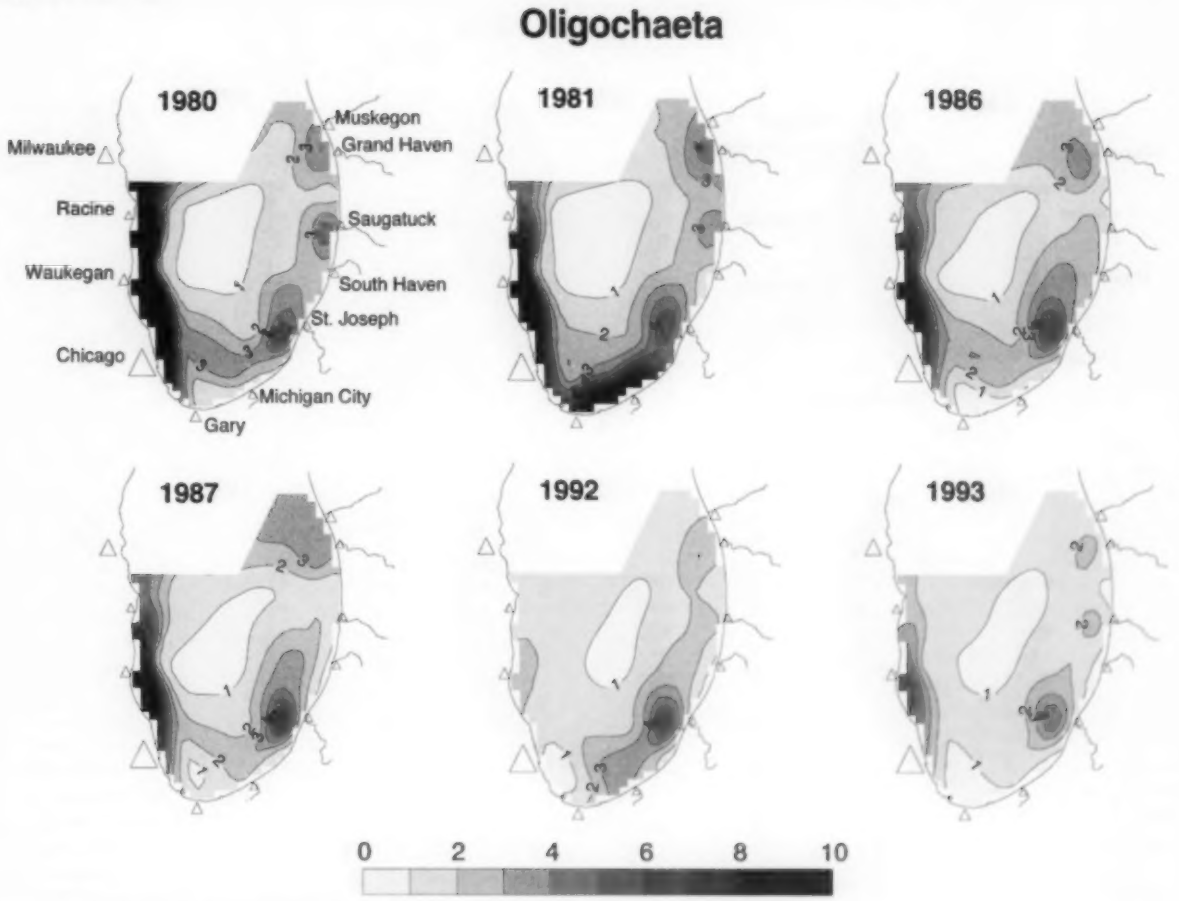
Fig. 2 (*continued*).



populations. *Dreissena polymorpha* was first reported from Lake Michigan in 1989 in the nearshore region near Chicago and by 1993 had colonized all hard substrates within about 7 km from shore from Waukegan to Michigan City (Marsden et al. 1993). In 1993, mean densities ranged from 50 000 to about 100 000·m^{-2} on the extensive reefs and shoals in this region (Marsden et al. 1993). None of our sites were located in this area (Ponar grab cannot sample in hard substrate areas), so densities of *D. polymorpha* in our surveys were not representative of overall densities within the southern basin. Nevertheless, our surveys in 1992 and 1993 do provide a measure of relative distributions and abundances. *Dreissena polymorpha* was found at all sites in the 16–30 m interval in both 1992 and 1993, with densities generally higher in the later year (Fig. 4). Densities in 1993 were <500·m^{-2} except at station V-1, where mean densities were 2889·m^{-2} in 1992 and 18 906·m^{-2} in 1993. Of the 12 sites in the 31–50 m interval, *D. polymorpha* was collected at five sites in 1992 and at 10 sites in 1993 (maximum mean density 133·m^{-2}), and of the 11 sites in the 51–90 m interval, *D. polymorpha* was collected at one site in 1992 and at three sites in 1993 (maximum mean density 9·m^{-2}). *Dreissena polymorpha* was not found at sites deeper than 90 m.

Discussion

Declines in densities of the three dominant macroinvertebrate groups, *Diporeia*, oligochaetes, and sphaeriids, at depths <50 m in southern Lake Michigan between 1980 and 1993 basically reverse a trend of increasing densities that occurred between 1930 and 1964 (Robertson and Alley 1966) and between the mid-1960s and 1980–1981 (Nalepa 1987). These declines correlate well with decreasing trends in phosphorus loads and pelagic productivity over the same time period. After phosphorus control measures were initiated in the mid-1970s, loads declined in the 1980s and remained lower through 1993 (Johengen et al. 1994; IJC, Windsor, Ont., unpublished data), and phosphorus concentrations decreased between the late 1970s and the early 1980s (Scavia et al. 1986; Chang and Rossman 1988), as did the intensity of the spring diatom bloom (Vandercastle 1985). Dated cores from the area of highest sedimentation in the southern basin show a similar trend: phosphorus concentrations in the sediment declined through the 1980s after a peak in the late 1960s – early 1970s (T. Johengen, Cooperative Institute for Limnology and Ecosystems Research, unpublished data). Also, primary productivity declined be-

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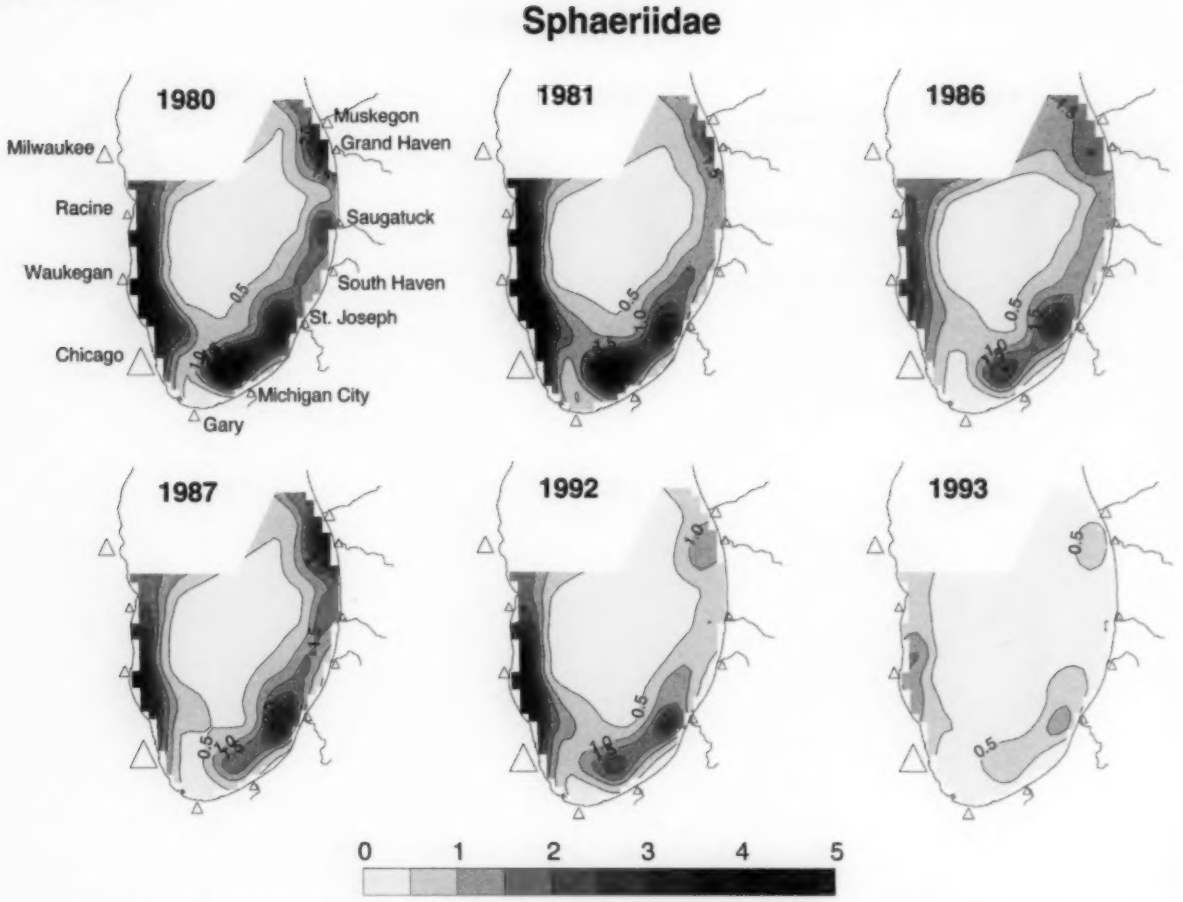
Fig. 2 (*concluded*).



tween the early 1980s and early 1990s (G.L. Fahnenstiel, Great Lakes Environmental Research Laboratory, personal communication); however, recent declines may be more related to the filtering activities of *D. polymorpha* than to phosphorus load reductions. With corresponding declines in macroinvertebrate densities through the 1980s and early 1990s, densities in 1993 were equal to or lower than densities found in the mid-1960s (Table 4).

In the period between 1980–1981 and 1986–1987, when productivity in Lake Michigan was declining and *D. polymorpha* was not yet present, the two groups that declined to the greatest extent in the nearshore region were oligochaetes and sphaeriids, while declines in *Diporeia* were minimal. The two former groups generally respond directly to changes in benthic food inputs (Wiederholm 1980; Clarke et al. 1997), but for *Diporeia*, other factors such as fish predation may complicate interpretations of relationships between benthic food inputs and abundances (Johnson and McNeil 1986; McDonald et al. 1990). When densities of all three groups increased two- to fivefold at depths <50 m between the mid-1960s and 1980–1981, Nalepa (1987) attributed the increases to enrichment and greater benthic food inputs but, in the case of *Diporeia*, provided evidence that suggested

Fig. 3. Region of the study area where *Diporeia* declined more than 60% between 1980–1981 and 1992–1993.

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Table 3. Mean densities (no.·m^{-2}) of oligochaete species in 1980–1981 and 1992–1993 in each of four depth intervals.

	16–30 m		30–50 m		50–90 m		90–156 m	
	1980–1981	1992–1993	1980–1981	1992–1993	1980–1981	1992–1993	1980–1981	1992–1993
Taxa								
Enchytraeidae	32	4	67	21	158	69	181	55
Lumbriculidae								
Stylodrilus heringianus (1)	1473	608	2974	1262	1216	1247	681	1010
Tubificidae								
Aulodrilus americanus (2)	14	97	<1	0	0	<1	0	0
A. limnobius (2)	2	0	0	0	0	0	0	0
A. pluriseta (2)	175	7	7	<1	0	0	0	0
Ilyocryptus freyi (2)	0	3	0	0	0	0	0	0
I. templetoni (2)	0	1	0	1	<1	0	0	0
Limnodrilus cervix (3)	1	0	0	0	0	0	0	0
L. claparadieanus (3)	2	1	0	<1	0	0	0	0
L. hoffmeisteri (3)	300	100	167	140	141	58	8	7
L. spiralis (3)	7	0	2	0	<1	0	<1	0
L. profundicola (1)	5	8	11	14	3	4	1	<1
L. udekemianus (3)	<1	<1	0	<1	0	0	0	0
Opisthonais serpentia	0	<1	0	0	0	0	0	0
Potamothrix moldaviensis (2)	21	8	46	68	1	<1	0	0
P. vejdovskyi (2)	295	58	439	387	17	35	0	<1
Quistrodrilus multisetosus (3)	117	1	<1	2	<1	0	0	0
Rhyacodrilus coccineus (1)	<1	<1	<1	4	0	0	0	0
Spirosperma ferox (2)	4	2	0	<1	0	<1	0	0
S. nikolskyi (1)	6	3	80	59	<1	2	<1	0
Tubifex ignotus	2	0	0	0	0	0	0	0
T. americanus (1)	0	<1	<1	9	2	1	1	<1
T. tubifex (3)	4	2	51	69	27	18	14	14
T. superiorensis (1)	2	1	2	<1	1	0	<1	0
Variechaetidrilus augustipenis (3)	8	21	0	1	0	<1	0	0
Immatures without hair setae	3253	683	936	1005	426	256	28	24
Immatures with hair setae	211	49	211	788	142	94	84	42
Naididae (11 species)[a]	69	31	2	0	1	<1	<1	0
Type 1	1486 (24.8)	620 (36.7)	3067 (61.4)	1348 (35.2)	1222 (57.3)	1254 (70.3)	683 (68.4)	1010 (87.7)
Type 2	511 (8.5)	176 (10.4)	492 (9.8)	456 (11.9)	18 (0.8)	35 (2.0)	0 (0.0)	<1 (<0.1)
Type 3	439 (7.3)	125 (7.4)	220 (4.4)	212 (5.5)	168 (7.9)	76 (4.3)	22 (2.2)	21 (1.8)
Other	3567 (59.4)	767 (45.4)	1216 (24.3)	1812 (47.3)	727 (34.1)	419 (23.5)	293 (29.4)	121 (10.5)
Total	6003	1688	4995	3828	2135	1784	998	1152

Note: The type category of each species is given in parentheses next to the species name (see text for explanation of categories). Also given is the percentage of individuals (in parentheses) in each of three trophic categories.

[a]*Arcteonais lomondi, Chaetogaster diaphanus, Nais alpina, Nais elinguis, Nais simplex, Nais variabilis, Piguetiella michiganensis, Stylaria fossularius, Stylaria lacustris, Uncinata uncinais, Vejdovskyella intermedia.*

decreased fish predation was also a factor. In the Bay of Quinte, oligochaetes and sphaeriids declined in response to phosphorus reductions, but a noted increase in *Diporeia* was attributed to the collapse of the white perch (*Morone americana*) population (Johnson and McNeil 1986). In adjacent Lake Ontario, where white perch populations were never abundant, declines in standing stocks of *Diporeia* were similar to those for oligochaetes and sphaeriids.

In our study, each of the three groups continued to decline between 1986–1987 and 1992–1993. While decline rates in oligochaetes and sphaeriids over this period were generally comparable with decline rates in 1980–1981 to 1986–1987,

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Fig. 4. Distribution and density (no.·m^{-2}) of the zebra mussel *Dreissena polymorpha* in 1992 and 1993. Note log scale.

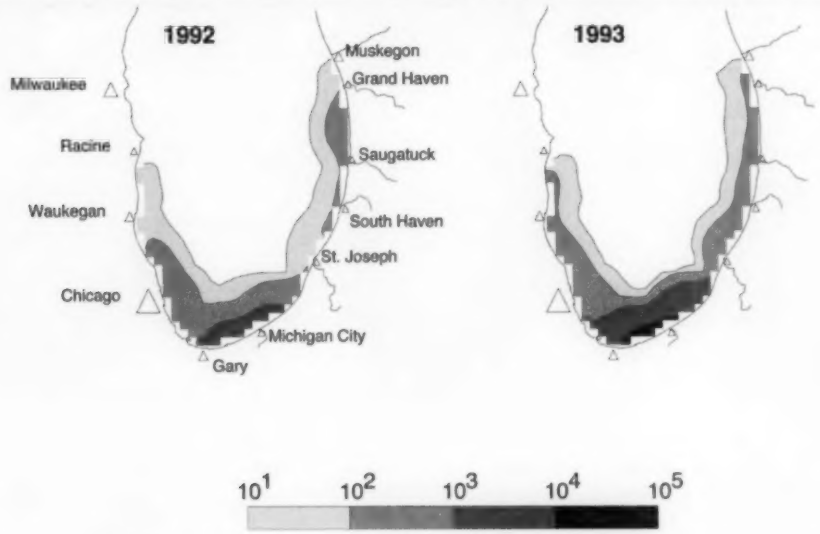

Table 4. Mean (± SE) density (no.·m^{-2}) of the three major macroinvertebrate groups at different depth intervals in 1962–1967 and 1993.

	1962–1967	1993	*P*
Depth: 16–30 m			
Diporeia	3 061±962	2158±847	ns
Oligochaeta	2 090±983	1599±827	ns
Sphaeriidae	1 860±1251	508±213	ns
Total	7 011	4265	
Depth: 31–50 m			
Diporeia	6 361±921	5648±1155	ns
Oligochaeta	4 096±903	2733±715	ns
Sphaeriidae	2 859±579	1273±399	<0.05
Total	13 316	9654	
Depth: 51–90 m			
Diporeia	3 974±374	5161±705	ns
Oligochaeta	1 690±591	1494±168	ns
Sphaeriidae	729±150	362±134	<0.05
Total	6 393	7017	
Depth: >90 m			
Diporeia	2 796±543	3372±940	ns
Oligochaeta	2 089±840	1040±237	ns
Sphaeriidae	178±48	106±68	<0.05
Total	5 063	4518	

Note: The 1962–1967 data were taken from Alley and Mozley (1975) and A.M. Beeton (Great Lakes Environmental Research Laboratory, unpublished data). Because sites were sampled at different frequencies in 1962–1967, SEs were derived from station means. n = 10 (<30 m), n = 8 (31–50 m), n = 8 (51–90 m), and n = 5 (>90 m). Only stations sampled in both periods were included. Differences between periods were tested using the Wilcoxon matched-pairs signed-rank test. ns, not significant.

decline rates in *Diporeia* increased fivefold and were focused primarily in the south–southeastern portion of the lake. Since *D. polymorpha* became established in this area in 1989, we hypothesize that food competition with *D. polymorpha* may have led to accelerated declines in *Diporeia*. By 1993, *D. polymorpha* had heavily infested the south–southwestern portion of the lake, as extensive shoals and reefs in this area provided an ideal substrate for colonization (Marsden et al. 1993). Water clarity at many sites in this region increased twofold between 1990 and 1993 (Marsden et al. 1993), an increase similar to that found in other Great Lakes areas heavily infested by *D. polymorpha* (Fahnenstiel et al. 1995*a*). *Diporeia* relies on freshly sedimented organic matter as a food source (i.e., mostly diatoms), while *D. polymorpha* is a filter-feeder that intercepts this material before it actually settles to the bottom. In the profundal region of eastern Lake Erie, *Diporeia* declined 88% after *Dreissena* became established; also, there was a direct inverse relationship between numbers of *Diporeia* and *Dreissena* in individual samples (Dermott and Kerec 1997). In 1992–1993, *D. polymorpha* was not abundant at most sites in the southeastern region. However, with a counterclockwise circulation pattern in southern Lake Michigan, extensive *D. polymorpha* populations in the south–southwestern portion of the lake may have affected *Diporeia* populations in areas to the east. Changes in water clarity and pelagic productivity have been observed in areas with low *D. polymorpha* populations when circulation patterns integrate waters from nearby areas with higher populations (Fahnenstiel et al. 1995*a*). Also, since physical processes readily resuspend and transport organic matter from nearshore to offshore areas in the southern basin (Eadie et al. 1984), we suspect that the filtering activities of extensive *D. polymorpha* populations in shallow, nearshore areas are causing decreased benthic inputs to *Diporeia* in deeper areas.

Many species of fish feed heavily on *Diporeia*, and changes in *Diporeia* densities have been related to shifts in fish communities and predation pressure (Johnson and McNeil 1986; McDonald et al. 1990). Thus, the role of fish predation in causing observed changes in *Diporeia* densities must be examined. Between 1980–1981 and 1992–1993, a number of changes occurred in the nearshore fish communities of Lake Michigan. In the early years of this period, the decline in alewife (*Alosa pseudoharengus*), which began in

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the 1970s, continued, while yellow perch (*Perca flavescens*) and bloater (*Coregonus hoyi*) increased (Jude and Tesar 1985; Fabrizio et al. 1995). McDonald et al. (1990) found a twofold decline in *Diporeia* densities between 1979–1980 and 1984–1985 in the southern basin and attributed this decline to increased predation from perch and bloater. We did not sample in 1984 or 1985, but benthic samples were taken at one of our sites (H-31) in these same two years (M.A. Quigley, Great Lakes Environmental Research Laboratory, unpublished data). H-31 is located off Grand Haven, Mich., in the same general location where McDonald et al. (1990) sampled. Mean densities of *Diporeia* at this site in 1980, 1981, 1984, 1985, 1986, and 1987 were 10 362, 10 048, 7519, 7815, 9354, and 10 687·m^{-2}, respectively. Densities at this site do indeed appear lower in 1984 and 1985, which agrees with the findings of McDonald et al. (1990). However, note that densities in 1986–1987 were similar to densities in 1980–1981, so any predation effects appear to have been temporary. Also, minimal declines in *Diporeia* between 1980–1981 and 1986–1987 at <50 m suggest that potential increases in fish predation (at least from perch and bloater) had little impact on overall densities. In the period between 1986–1987 and 1992–1993, yellow perch declined dramatically in the southern basin, while bloater and other fish species that feed heavily on *Diporeia* declined or remained fairly stable (Fabrizio et al. 1995). Given that the greatest declines in *Diporeia* occurred over this period (Table 2), it appears that changes in fish predation cannot account for the observed declines.

Unlike *Diporeia*, declines in oligochaetes and sphaeriids in the south–southeastern portion of the study area were not significantly different from declines in other areas, implying minimal *D. polymorpha* impacts. For oligochaetes, these findings are consistent with those in eastern Lake Erie where oligochaete densities were unaffected by the presence of *Dreissena* (Dermott and Kerec 1997). Oligochaetes are infaunal detritivores that are not as dependent on freshly settled material as *Diporeia* (Gardner et al. 1985) and potentially utilize *D. polymorpha* feces and pseudofeces as a food source. In some studies, oligochaete densities actually increased after *D. polymorpha* became established (Stewart and Haynes 1994). Decreased oligochaete densities between 1980–1981 and 1992–1993 in our study area would therefore indicate a true response to declines in nutrient loads and overall productivity. The relative proportion of the oligotrophic indicator *S. heringianus* did increase at three of the four depth intervals, which is consistent with a shift to more oligotrophic conditions. The reason for the contrary trend at the 31–50 m interval is not clear. Although total oligochaete densities at this depth interval declined, there was an increase in densities of *Tubifex tubifex* and immatures of the type with hair setae, most likely immatures of this species. *Tubifex tubifex* is considered a eutrophic indicator species but also does well in oligotrophic waters (Milbrink 1983). When oligochaete densities increased between the mid-1960s and 1980–1981, an overall shift in species composition did not occur (Nalepa 1987).

For sphaeriids, our findings in Lake Michigan contrast with those in Lake Erie where this group declined dramatically in areas where *D. polymorpha* was abundant (Dermott and Kerec 1997). Of the three major groups, sphaeriids were the least abundant, and declined the most, at all of our depth intervals. With such a marked decline in sphaeriids throughout the study area, regional declines specific to *D. polymorpha* impacts may have been difficult to discern. Also, the dominant sphaeriid genus in the southern basin is *Pisidium* (Nalepa et al. 1985). This genus occurs in the upper sediments and feeds by filtering suspended microorganisms from interstitial waters (Lopez and Holopainen 1987). Thus, like oligochaetes, it is not dependent on freshly settled algal material as a direct source of food.

Macroinvertebrate densities declined to the greatest extent at depths <30 m, were less pronounced at 30–50 m, and were minimal at depths >50 m. A similar depth-dependent response was apparent when densities increased between the mid-1960s and 1980–1981 (Nalepa 1987). Such a benthic response might be expected, as pelagic productivity is greater and more closely integrated with nutrient inputs in nearshore waters compared with offshore (Ladewski and Stoermer 1973; Schelske et al. 1980). At the shallowest interval, rates of decline in oligochaetes and sphaeriids were greater early in the study period (1980–1981 to 1986–1987) compared with later (1986–1987 to 1992–1993), indicating a rapid early response to load reductions. In reality, declines might have been observed earlier if densities had been documented in the 1970s. At the 31–50 m interval, rates of decline were greater in the later time period, indicating more of a delayed response to productivity declines. At the very least, observed declines in both the 16–30 and 31–50 m intervals seemed consistent with the turnover time of bottom particulate material in the southern basin, which is estimated to be 9 years at 12 m, 16 years at 65 m, and 23 years at 100 m (Robbins et al. 1998).

Oligochaetes and sphaeriids were not uniformly distributed throughout the study area at depths <50 m; higher densities were found near Waukegan and in the depositional basins of the southeastern portion of the lake (Fig. 3). Despite these spatial differences, density declines occurred to a similar extent throughout the study area. This apparent inconsistency is likely a reflection of the high degree of mixing and materials transport that occurs within the nearshore of the southern basin (Chambers and Eadie 1981; Eadie et al. 1984). Within this region, particulate material is constantly being redistributed by storms and longshore currents before being transported to deeper waters. Resuspension occurs on the order of weeks or months, while transport occurs over years. These physical processes greatly influence spatial distributions of macroinvertebrate communities in the nearshore (Stimpson et al. 1975; Winnell and White 1985).

Most permanent deposition of particulate material in Lake Michigan occurs at depths >50 m (Edgington and Robbins 1975). Because of the integrative nature of food inputs to this deep region, 60–100 m has been suggested as the best sampling depth interval to monitor trends in benthic populations relative to the changing trophic status of the lake (Winnell and White 1985). This may be true over the long term, but the response of the macroinvertebrate community to trophic changes occurs more slowly at these depths, and therefore, longer time periods between surveys are needed to detect changes. In the 13-year time interval of this study, declines were apparent for all groups at depths <50 m, but only sphaeriids declined at depths >50 m. Similarly, in the ap-

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proximately 15-year time period between the mid-1960s and 1980–1981, all groups increased at depths <50 m, but only oligochaetes increased at depths >50 m (Nalepa 1987). With the relatively long turnover time of benthic particulate material at deeper depths, our inability to detect consistent changes in all groups was likely a result of the short time span between our surveys. Robertson and Alley (1966) found that *Diporeia*, oligochaetes, and sphaeriids increased in the deeper waters of Lake Michigan between 1931 and 1964, a time span of 33 years.

In summary, densities of the three dominant macroinvertebrate groups in southern Lake Michigan declined dramatically between the early 1980s and early 1990s at depths <50 m; by 1993, densities were equal to or lower than densities found in the mid-1960s. Both reductions in phosphorus loads and the filtering activities of *D. polymorpha* likely played a role in this decline. Oligochaetes and sphaeriids were most impacted by nutrient reductions, while *Diporeia* was apparently most impacted by *D. polymorpha*. Of utmost concern is the decline in *Diporeia* populations in the southeast region of the lake where numbers at many sites <50 m were approaching zero in 1993. As *D. polymorpha* spreads and becomes increasingly abundant, further declines in *Diporeia* populations may be expected. Further declines are also imminent if the other *Dreissena* species, *Dreissena bugensis*, becomes established on the soft, offshore sediments of Lake Michigan as it has in lakes Erie and Ontario (Mills et al. 1993; Dermott and Kerec 1997). Because *Diporeia* accounts for a major portion of benthic invertebrate biomass in Lake Michigan (Nalepa 1989) and is a major energy link between pelagic production and fish (Gardner et al. 1990), declines in *Diporeia* over large areas will likely lead to serious disruptions in the Lake Michigan food web.

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References

Alley, W.P., and Mozley, S.C. 1975. Seasonal abundance and spatial distribution of Lake Michigan macrobenthos, 1964–67. Great Lakes Research Division Spec. Publ. 54, University of Michigan, Ann Arbor, Mich.

Botts, P.S., Patterson, B.A., and Schloesser, D.W. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? J. N. Am. Benthol. Soc. **15**: 179–184.

Chambers, R.L., and Eadie, B.J. 1981. Nepheloid and suspended particulate matter in south-eastern Lake Michigan. Sedimentology, **28**: 439–447.

Chang, W.Y.B., and Rossman, R. 1988. Change in the abundance of blue green algae related to nutrient loadings in the nearshore of Lake Michigan. Hydrobiologia, **157**: 271–278.

Chapra, S. 1977. Total phosphorus model for the Great Lakes. 1977. J. Environ. Eng. Div. **103**: 147–161.

Clarke, K.D., Knoechel, R., and Ryan, P.M. 1997. Influence of trophic role and life-cycle duration on timing and magnitude of benthic macoinvertebrate response to whole-lake enrichment. Can. J. Fish. Aquat. Sci. **54**: 89–95.

Cook, D.G., and Johnson, M.G. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. J. Fish. Res. Board Can. **31**: 763–782.

Dermott, R., and Kerec, D. 1997. Changes in the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. Can. J. Fish. Aquat. Sci. **54**: 922–930.

Eadie, B.J., Chambers, R.L., Gardner, W.S., and Bell, G.L. 1984. Sediment trap studies in Lake Michigan: resuspension and chemical fluxes in the southern basin. J. Great Lakes Res. **10**: 307–321.

Edgington, D.N., and Robbins, J.A. 1975. The behavior of plutonium and other long-lived radionuclides in Lake Michigan. II. Patterns of deposition in the sediments. *In* Impact of nuclear releases into the aquatic environment. IAEA, Vienna, Austria. pp. 245–260.

Edsall, T.A., and Charlton, M.N. 1996. Nearshore waters of the Great Lakes. Background Paper, State of the Lakes Ecosystem Conference '96, Environment Canada–U.S. EPA, EPA 905-D-96-001b.

Fabrizio, M.C., Ferreri, C.P., and Hansen, M.J. 1995. Prey fish communities as indicators of ecosystem health in Lake Michigan. Project Completion Report to the Environmental Protection Agency. Great Lakes Science Center, U.S. Geological Survey, Ann Arbor, Mich.

Fahnenstiel, G.L., Lang, G.A., Nalepa, T.F., and Johengen, T.H. 1995*a*. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. J. Great Lakes Res. **21**: 435–448.

Fahnenstiel, G.L., Bridgeman, T.B., Lang, G.A., McCormick, M.J., and Nalepa, T.F. 1995*b*. Phytoplankton productivity in Saginaw Bay, Lake Huron: effects of zebra mussel (*Dreissena polymorpha*) colonization. J. Great Lakes Res. **21**: 465–475.

Gardner, W.S., Nalepa, T.F., Frez, W.A., Cichocki, E.A., and Landrum, P.F. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. Can. J. Fish. Aquat. Sci. **42**: 1827–1832.

Gardner, W.S., Quigley, M.A., Fahnenstiel, G.L., Scavia, D., and Frez, W.A. 1990. *Pontoporeia hoyi* — a direct trophic link between spring diatoms and fish in Lake Michigan. *In* Large lakes: ecological structures and functions. *Edited by* M.M. Tilzer and C. Serruya. Springer-Verlag, Berlin, Germany.

Johengen, T.H., Johannsson, O.E., Pernie, G.L., and Millard, E.S. 1994. Temporal and seasonal trends in nutrient dynamics and biomass measures in Lakes Michigan and Ontario in response to phosphorus control. Can. J. Fish. Aquat. Sci. **51**: 2570–2578.

Johnson, M.G., and McNeil, O.C. 1986. Changes in abundance and species composition in benthic macroinvertebrate communities of the Bay of Quinte, 1966–1984. *In* Project Quinte: point-source phosphorus control and ecosystem response in the Bay of Quinte, Lake Ontario. *Edited by* C.K. Minns, D.A. Hurley, and K.H. Nicholls. Can. Spec. Publ. Fish. Aquat. Sci. No. 86.

Jude, D.J., and Tesar, F.J. 1985. Recent changes in the inshore forage fish of Lake Michigan. Can. J. Fish. Aquat. Sci. **42**: 1154–1157.

Ladewski, T.B., and Stoermer, E.F. 1973. Water transparency of southern Lake Michigan in 1971 and 1972. Proceedings of the 16th Conference on Great Lakes Research. International Association for Great Lakes Research, Ann Arbor, Mich. pp. 791–807.

Lang, C., and Reymond, O. 1992. Reversal of eutrophication in

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Lake Geneva: evidence from the oligochaete communities. Freshwater Biol. **28**: 145–148.

Lauritsen, D.D., Mozley, S.C., and White, D.S. 1985. Distribution of oligochaetes in Lake Michigan and comments on their use as indices of pollution. J. Great Lakes Res. **11**: 67–76.

Lopez, G.R., and Holopainen, I.J. 1987. Interstitial suspension-feeding by *Pisidium* spp. (Pisidiidae:Bivalvia): a new guild in the lentic benthos? Am. Malacol. Bull. **5**: 21–30.

Marsden, J.E., Trudeau, N., and Keniry, T. 1993. Zebra mussel study of Lake Michigan. Aquat. Ecol. Tech. Rep. 93/14, Illinois Natural History Survey, Zion, Ill.

McDonald, M.E., Crowder, L.B., and Brandt, S.B. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: a response to shifts in the fish community. Limnol. Oceanogr. **35**: 220–227.

Milbrink, G. 1983. An improved environmental index based on the relative abundance of oligochaete species. Hydrobiologia, **102**: 89–97.

Mills, E.L., Dermott, R.M., Roseman, E.F., Dustin, D., Mellina, E., Conn, D.B., and Spidel, A. 1993. Colonization, ecology, and population structure of the "quagga mussel" in the lower Great Lakes. Can. J. Fish. Aquat. Sci. **50**: 2305–2314.

Nalepa, T.F. 1987. Long term changes in the macrobenthos of southern Lake Michigan. Can. J. Fish. Aquat. Sci. **44**: 515–524.

Nalepa, T.F. 1989. Estimates of macroinvertebrate biomass in Lake Michigan. J. Great Lakes Res. **15**: 437–443.

Nalepa, T.F., Quigley, M.A., Childs, K.F., Gauvin, J.M., Heatlie, T.S., Parker, M.P., and Vanover, L. 1985. Macrobenthos of southern Lake Michigan, 1980–81. NOAA Data Rep. ERL GLERL-28. Great Lakes Environmental Research Laboratory, Ann Arbor, Mich.

Nalepa, T.F., Hartson, D.J., Gostenik, G.W., Fanslow, D.L., and Lang, G.A. 1996. Changes in the freshwater mussel community of Lake St. Clair: from Unionidae to *Dreissena polymorpha* in eight years. J. Great Lakes. Res. **22**: 354–369.

Robbins, J.A., Eadie, B.J., and Edgington, D.N. 1998. Spatially variable, first order averaging of cesium-137 fluxes to sediments in Lake Michigan revealed by long-term changes in activities of benthic trap samples and sediments. Ocean Sciences Meeting. American Geophysical Union, San Diego, Calif. (Abstr.)

Robertson, D.M. 1997. Regionalized loads of sediment and phosphorus to Lakes Michigan and Superior — high flow and long-term average. J. Great Lakes Res. **23**: 416–439.

Robertson, A., and Alley, W.P. 1966. A comparative study of Lake Michigan macrobenthos. Limnol. Oceanogr. **11**: 576–583.

Saether, O.A. 1980. The influence of eutrophication on deep lake benthic invertebrate communities. Prog. Water Technol. **12**: 161–180.

Scavia, D., Fahnenstiel, G.L., Evans, M.S., Jude, D.J., and Lehman, J.T. 1986. Influence of salmonid predation and weather on long-term water quality trends in Lake Michigan. Can. J. Fish. Aquat. Sci. **43**: 435–443.

Schelske, C.L. 1978. Detecting trends in Great Lakes water quality. *In* The Great Lakes. 2. Water Qual. Bull. Vol. 3. Canada Centre for Inland Waters, Burlington, Ont.

Schelske, C.L., Feldt, L.E., and Simmons, M.S. 1980. Phytoplankton and physical–chemical conditions in selected rivers and the coastal zone of Lake Michigan, 1972. Great Lakes Research Division Publ. 19, University of Michigan, Ann Arbor, Mich.

Schloesser, D.W., Reynoldson, T.B., and Manny, B.A. 1995. Oligochaete fauna of western Lake Erie 1961 and 1982: signs of sediment quality recovery. J. Great Lakes Res. **21**: 294–306.

Stewart, T.W., and Haynes, J.M. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of *Dreissena polymorpha*. J. Great Lakes Res. **20**: 479–493.

Stimpson, K.S., Brice, J.R., Barbour, M.T., and Howe, P. 1975. Distribution and abundance of inshore oligochaetes in Lake Michigan. Trans. Am. Microsc. Soc. **94**: 384–394.

Vandercastle, J.R. 1985. A study of long-term changes of the phytoplankton community and seasonal changes in alkaline phosphate activity observed in Lake Michigan. Ph.D. thesis, University of Wisconsin, Milwaukee, Wis.

Wiederholm, T. 1980. Use of benthos in lake monitoring. J. Water Pollut. Control Fed. **52**: 537–547.

Winnell, M.H., and White, D.S. 1984. Ecology of shallow and deep water populations of *Pontoporeia hoyi* (Smith) (Amphipoda) in Lake Michigan. Freshwat. Invertebr. Biol. **3**: 118–138.

Winnell, M.H., and White, D.S. 1985. Trophic status of southeastern Lake Michigan based on the Chironomidae (Diptera). J. Great Lakes Res. **11**: 540–548.

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Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size

James E. Garvey, Russell A. Wright, and Roy A. Stein

Abstract: How large size affects overwinter growth and survival of age-0 fish may vary as a function of food, predation, and energetic condition. During two winters in Ohio, we assessed how these factors affected growth and survival of varying sizes of age-0 largemouth bass (*Micropterus salmoides*) by combining a field survey (N = 2 reservoirs) with multiscale experiments (reservoirs, ponds, outdoor pools). In our survey, more small (<100 mm total length) individuals died by spring in one reservoir than in the other. Similarly, when we stocked two reservoirs with marked age-0 largemouth bass in fall, mortality of small individuals was higher in one system overwinter, potentially due to differences in predation intensity. In ponds during two winters, size-selective mortality of small largemouth bass occurred in only two of eight ponds, potentially as a function of cannibalism. Varying ration in pools (starved, 0.5× maintenance, or 1.5× maintenance) did not affect survival, even though starved individuals lost substantial wet weight and energy content. Only when predators were present did small individuals die at high rates, although energy depletion may have contributed to predatory mortality. To increase the probability of overwinter survival, managers should seek to improve first-summer growth, reduce winter predation, and increase winter forage.

Résumé : Chez le poisson d'âge-0, l'influence de la taille sur la croissance et la survie en hiver varie en fonction de la nourriture, de la prédation et de l'état énergétique. Pendant deux hivers en Ohio, nous avons cherché à déterminer comment ces facteurs influent sur la croissance et la survie de l'achigan à grande bouche (*Micropterus salmoides*) d'âge-0 de différentes tailles en combinant les résultats d'un relevé sur le terrain (N = 2 réservoirs) à ceux d'expériences à diverses échelles (réservoirs, étangs et mares). D'après le relevé, le nombre de spécimens de petite taille (longueur totale <100 mm) morts au printemps était plus élevé dans un des deux réservoirs étudiés. Nous avons ensemencé en automne deux réservoirs en y lâchant des achigans marqués d'âge-0; dans ce cas aussi, la mortalité des petits sujets était plus importante dans un des deux réservoirs à la fin de l'hiver, l'écart étant peut-être dû à une différence d'intensité de prédation. Par ailleurs, nous avons étudié huit étangs durant deux hivers et nous n'avons constaté de mortalité chez les achigans de petite taille que dans deux d'entre eux; la mortalité observée pourrait avoir été due au cannibalisme. Nous avons soumis les populations des mares à des régimes alimentaires différents (jeûne, demi-ration d'entretien ou une fois et demi la ration d'entretien) : le régime alimentaire n'a pas influé sur la survie et ce, malgré une baisse considérable du poids humide et de la teneur énergétique chez les sujets soumis au jeûne. Chez les achigans de petite taille, la mortalité n'a été élevée que dans les mares où il y avait des prédateurs; la baisse d'énergie a toutefois pu contribuer à la mortalité par prédation. Pour augmenter les chances de survie de l'achigan, les gestionnaires doivent prendre des mesures pour améliorer la croissance des poissons en été et pour réduire la prédation en hiver, et augmenter les rations en hiver.

[Traduit par la Rédaction]

Introduction

Conventional wisdom holds that body size is strongly linked to growth and survival of early life stages (e.g., Miller et al. 1988). For larval and juvenile fishes, large size confers a host of advantages during a time when mortality is typically high, including reduced risk of predation through improved swimming ability (Christensen 1996), reduced vulnerability to gape-limited predators (Hambright et al. 1991), and reduced risk of starvation through enhanced foraging opportunities (Schael et al. 1991; Bremigan and Stein 1994). When food is scarce, large fish have abundant energy reserves relative to small counterparts (Isely 1981; Ludsin and DeVries 1997), thereby improving their survival. Both starvation and predation are important, often interacting during the first year of life to influence survival of small larval

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and juvenile fishes (Rice et al. 1987), recruitment to later life stages, and, ultimately, cohort strength.

Starvation and, perhaps, predation may be especially important during the first winter when, for many fish, rapid summer growth and large fall size are necessary for survival (Post and Evans 1989; Cargnelli and Gross 1996). Hence, the first winter often is quite commonly viewed as a "critical period" determining year class strength of fishes (May 1974). As with other fishes, large fall size often improves winter survival of largemouth bass (*Micropterus salmoides*) (Miranda and Hubbard 1994*a*, 1994*b*; Ludsin and DeVries 1997). Although size-dependent energy depletion has often been suggested as the sole factor determining overwinter success (Gutreuter and Anderson 1985), predation has recently been identified as important (Miranda and Hubbard 1994*b*). Because small largemouth bass do not always suffer high mortality during winter (Kohler et al. 1993; Wright 1993), the size-specific effects of starvation and predation as well as other sources of mortality for largemouth bass (e.g., disease) may vary among systems and years.

As with many fish species, growth during the first year of life varies greatly for largemouth bass (Adams and DeAngelis 1987; Garvey and Stein 1998). Thus, understanding how size-dependent processes drive overwinter survival is especially important for predicting their recruitment to the second year of life. Our goal, then, was to determine (*i*) if current models based solely on the interaction between size and energy depletion were sufficient for predicting overwinter mortality (e.g., Shuter et al.1980) or (*ii*) if models must incorporate other effects such as variable food availability and predation. We conducted a field survey plus experiments at multiple scales during the winters of 1994–1995 and 1995–1996 to assess the relative influence of size, food availability, predation, and energetic condition on growth and survival of juvenile largemouth bass. In our field survey, we explored how overwinter survival of largemouth bass varied between two Ohio reservoirs. In experiments in which age-0 largemouth bass were stocked into reservoirs and hatchery ponds, individuals were followed through winter in systems in which predators were abundant (reservoirs) or absent (ponds). We also conducted experiments in large outdoor pools to assess how food availability influenced overwinter survival.

Methods

General

Unless otherwise specified, all largemouth bass in surveys and experiments were (*i*) age-0 and (*ii*) measured (nearest 1 mm total length) and weighed (nearest 0.1 g, at least five individuals per 10-mm length class). Herein, age-0 begins when individuals hatch (usually May) and ends when the next year class hatches. For experiments, largemouth bass were obtained from Hebron State Fish Hatchery, Ohio (parental stock was obtained from Grand Lake St. Marys, Auglaize County, Ohio). In reservoirs and experiments, winter temperatures were quantified four or five times daily with a temperature data logger. Because energy depletion due to starvation may contribute to overwinter mortality (e.g., Oliver et al. 1979), we quantified energy content (kilojoules) of largemouth bass in experiments conducted in winter 1995–1996 using bomb calorimetry (see Rand et al. 1994 for specific methods). For each experiment, we quantified energy content of four to six largemouth bass per 10-mm length class. Largemouth bass >150 mm were verified as age-0 by examining scales. When sample sizes were sufficiently large ($N > 25$), we determined how age (either age-0 or age-1) varied as a function of the independent variable, length, using logistic regression (PROC LOGISTIC, SAS Institute Inc. 1985; Feinberg 1980). From this, we calculated the size-based probability of age and removed corresponding proportions of age-1 individuals from distributions.

Reservoir patterns

We determined how variation in size of naturally produced largemouth bass influences their overwinter survival in two Ohio reservoirs, Knox Lake (225 ha, 19.2 km of shoreline, Knox County) and Pleasant Hill Reservoir (344 ha, 21.5 km of shoreline, Richland and Ashland counties). In summer 1994, these reservoirs contained high densities of age-0 largemouth bass with widely varying fall sizes (50–200 mm). On 4 days during October 12–26, 1994, and 4 days during April 6–20, 1995, in Knox Lake, we collected largemouth bass by electrofishing (pulsed DC) littoral zones, sampling about 75% of the shoreline each day. Because different sizes of largemouth bass can occupy different depths, we sampled by driving the boat perpendicularly from deep (>1 m) to shallow (about 25 cm) water. On November 11, 1994, and April 25 and May 5, 1995, in Pleasant Hill Reservoir, we electrofished littoral zones in a similar fashion for 100 min/date.

Reservoir experiments

To estimate growth and mortality, thereby improving control over our reservoir survey, we stocked two Ohio reservoirs (both with historically low densities of age-0 largemouth bass) with marked, hatchery-reared largemouth bass (see general methods) of different sizes in fall 1995. Stocking densities were based on naturally occurring densities of largemouth bass in Knox Lake in 1994 (about 1.5 age-0 largemouth bass/m shoreline, J.E. Garvey, unpublished data). In Kokosing Lake (65 ha, 7.5 km of shoreline, Knox County), we stocked 4905 small (76–94 mm) and 5954 large (95–150 mm) age-0 largemouth bass of which 65 and 58% of small and large size classes received left and right pelvic fin clips, respectively. In Clark Lake (40 ha, 4.5 km of shoreline, Clark County), we stocked 7500 small (70–121 mm) and 284 large (146–267 mm) largemouth bass marked with pelvic fin clips (as for Kokosing Lake). For the Clark Lake stocking, we also marked all large and 65% of small largemouth bass with fluorescent yellow or red plastic granules (300 μm in diameter) sprayed with pressurized nitrogen at 70 g/cm^2 (see Nielsen 1992). Colored grains embedded under scales were detected with ultraviolet light. Mortality was negligible; after 24 h in hatchery raceways, only one of 6850 spray-marked largemouth bass died. With the exception of the large size class in Clark Lake for which lengths of all individuals were recorded (nearest 1 mm), we recorded lengths of about 10% of individuals. All individuals were measured for assignment to size classes.

Largemouth bass were stocked into Clark Lake and Kokosing Lake on October 26 and 27, 1995, respectively. Reservoirs were electrofished 1 week poststocking (1 day/reservoir) and during late April through early May 1996 (4 days/reservoir), sampling >70% of the shoreline each day. In fall, density of age-0 largemouth bass was estimated with a Petersen estimate for a single mark–recapture (Ricker 1975). In spring, captured largemouth bass were fin-clipped; their abundances were estimated with a modified Schnabel estimate for multiple censuses (Ricker 1975). During fall and spring electrofishing, we sampled predator diets (all piscivorous fish >250 mm) with gastric lavage (Seaburg 1957). Diets were collected in fine-mesh bags, preserved in 95% ethanol, identified to species for fish and to family for invertebrates, and measured (nearest 1 mm). If fish were digested beyond recognition, we iden-

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tified them to species using vertebral counts (Holland-Bartels et al. 1990).

Pond experiments

We conducted pond experiments during the winters of 1994–1995 and 1995–1996 to assess (*i*) the influence of size and food availability on overwinter survival without adult predators and (*ii*) mark retention. On October 19, 1994, we added 210–265 small (64–107 mm) and 105–135 large (115–179 mm) largemouth bass to each of four, 0.4-ha hatchery ponds (1.5 m average depth, 300–400 largemouth bass/pond; pond experiment A), recording lengths of all individuals. To provide additional forage, we added about 1700 fathead minnow (*Pimephales promelas*) (mean ± 1 SD length = 63 ± 7 mm, mean weight = 2.7 ± 1.0 g) to each pond. On June 14, 1995, we slowly drained each pond over 24 h and then recovered largemouth bass. To compare our ability to recover small and large largemouth bass, we added 102 (± 2) small and 100 (± 2) large marked individuals to two ponds (about 200 largemouth bass/pond; pond experiment B) 24 h after pond experiment A. We then drained these ponds over 24 h, recovering largemouth bass in a similar fashion to pond experiment A.

On October 25, 1995, we conducted pond experiment C to parallel reservoir experiments (see reservoir experiment methods) by adding 200–300 small (73–122 mm) and 25–50 large (142–268 mm) largemouth bass with no fish prey to each pond (N = 4 ponds, 250–325 largemouth bass/pond). To assess spray-mark retention, we stocked two of these ponds with spray-marked small and large largemouth bass (as in the reservoir experiment). In the remaining two ponds, small and large largemouth bass were fin-clipped (as in the reservoir experiment). Because these largemouth bass derived from the same group stocked into Clark Lake in fall 1995, we only counted small and large individuals stocked into each pond. On May 15, 1996, we drained ponds over 24 h and then recovered largemouth bass.

Pool experiments

To determine how food availability influences overwinter growth and survival of largemouth bass, we conducted an experiment in 2650-L flow-through, aerated outdoor pools at the Aquatic Ecology Laboratory, Ohio State University, in which we fed largemouth bass no food, a low ration, or a high ration (N = 3 pools/treatment) during winter 1995–1996. On October 30, 1995, we added 10 largemouth bass/pool (83–143 mm). Each pool contained ten 15-cm pieces of PVC pipe plus sparse leaf litter as shelter. Prey were fathead minnow (mean length = 52 ± 1 mm, mean weight = 1.4 ± 0.5 g), 36–63% of largemouth bass lengths. Low ration was 0.5× the wet weight (grams) estimated by a bioenergetics model for largemouth bass (Hewett and Johnson 1992) necessary to maintain their initial weight during the experiment (depending on temperature, 0.03–0.1 g·bass^{-1}·day^{-1}); high ration was 1.5× this maintenance level (0.1–0.3 g·bass^{-1}·day^{-1}). Temperatures for these simulations mimicked past winters in pools. Each week, we added sufficient fathead minnow (by wet weight) to provide these rations for the following 7 days. Remaining fathead minnow were removed only once in late December; thereafter, remaining fathead minnow were removed weekly immediately before prey addition. On January 14, March 6, and, finally, May 1, 1996, we partially drained pools, recovered largemouth bass with hand nets, measured and weighed them, and returned them to pools. Although we did not explicitly test for handling effects, survival of largemouth bass was high. In addition, growth in high-ration treatments was high, suggesting that handling effects were negligible (see Results).

Analyses

For the reservoir survey, we compared changes in length distributions of largemouth bass using a Kolmogorov–Smirnov test. In reservoir and pond experiments, we used G-tests to assess the relative loss of small and large largemouth bass by determining if observed relative proportions of marked fish differed from those originally stocked (Sokal and Rohlf 1981). For experiments in winter 1995–1996 in which we quantified energy content of largemouth bass, we compared both total energy content (kilojoules) and energy density (kilojoules per gram wet weight) across treatments with largemouth bass length as the covariate using analysis of covariance (ANCOVA). Because relationships between length and total energy content were power functions, we $\log_e(x)$ transformed both variables before analysis. After adjusting mean responses in ANCOVAs to the same values of the covariate, length (Neter et al. 1990), we used Scheffe's pairwise comparisons to compare differences between spring and fall total kilojoules or kilojoules per gram. For pool experiments, we quantified proportion change of largemouth bass wet weight during three periods: fall, winter, and spring. Pooling results across each feeding treatment, proportion change in weight as a function of length was analyzed using linear regression for each treatment–period combination (3 periods × 3 treatments = 9 comparisons). We also determined if weight change differed from zero using paired t-tests. For these nine tests, we adjusted α to protect against type I error ($\alpha/9 = 0.05/9 = 0.006$; Miller 1981).

Results

Temperatures

Both Pleasant Hill Reservoir (1994–1995) and Clark Lake (1995–1996) temperature recorders were lost. During winter 1994–1995, temperatures in Knox Lake and ponds were similar (Fig. 1A). During winter 1995–1996, temperatures were generally similar among Kokosing Lake and pools, although pools cooled more slowly in fall (Fig. 1B). During December 1995 through March 1996, daily temperatures in ponds were on average 1–2°C higher than in pools and Kokosing Lake (Fig. 1B).

Reservoir patterns

For Knox Lake, the likelihood of a largemouth bass being age-0 declined precipitously from 95% at 160 mm to 51% at 190 mm (logistic regression, $P < 0.05$, N = 65). Although individuals <125 mm comprised about 60% of the distribution in fall (Fig. 2A), this mode of small largemouth bass declined to 46% by spring, likely due to their differential mortality (Kolmogorov–Smirnov test, D = 0.18, $P < 0.05$; Fig. 2B). In Pleasant Hill Reservoir, aging by scales revealed that all of the largemouth bass ≤200 mm likely were age-0. Although about 66% of individuals were ≤125 mm in fall (Fig. 2C), their abundance declined to about 22% by spring (Kolmogorov–Smirnov test, D = 0.46, $P < 0.05$; Fig. 2D). Thus, mortality of small individuals appeared higher in Pleasant Hill Reservoir than in Knox Lake during winter 1994–1995.

Reservoir experiments

In Kokosing Lake, our fall 1995 stocking increased electrofishing catch per unit effort (CPE) to 1.7 largemouth bass/min shocking. Number of largemouth bass poststocking was 14 248 ± 1597 (Petersen estimate, mean ± 95% CI), resulting in about 1.9 age-0 largemouth bass/m shoreline (resident plus stocked). Relative proportions of small (<95 mm) and large (≥ 95 mm) marked largemouth bass captured in Kokosing Lake in fall 1995 did not differ from the initial propor-

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Fig. 1. Mean daily water temperature in Ohio reservoirs (solid line, squares), hatchery ponds (dotted line, circles), and pools (broken line, triangles) during the winters of 1994–1995 and 1995–1996. For clarity, symbols only are plotted for every 10th day. During 1994–1995, reservoir temperatures derive from Knox Lake. During 1995–1996, reservoir temperatures derive from Kokosing Lake. Temperature recorders for other reservoirs were lost during winter.

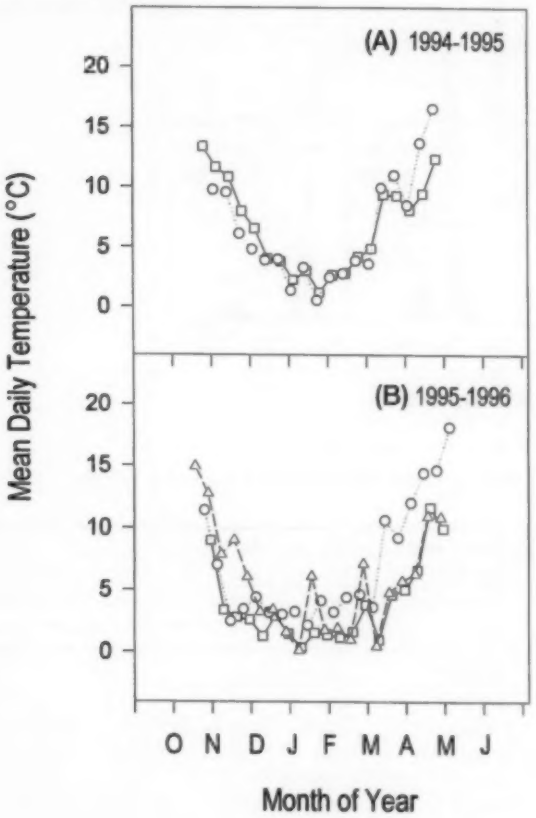
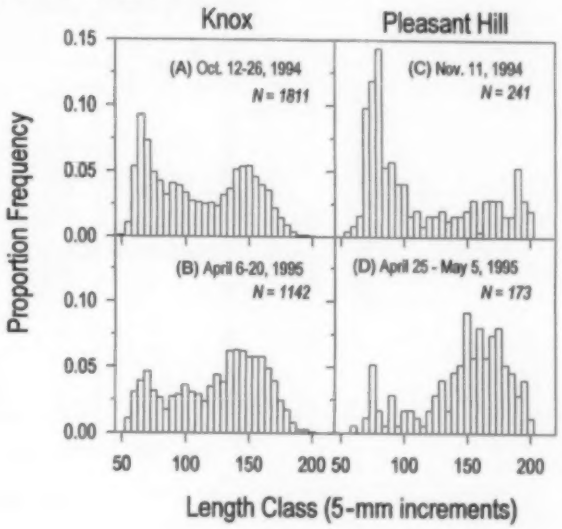


Fig. 2. Proportion of age-0 largemouth bass in each 5-mm length class captured by electrofishing in (A and B) Knox Lake Reservoir and (C and D) Pleasant Hill Reservoir, Ohio, in fall 1994 and spring 1995.



tion stocked a week earlier (G-test; G = 2.4, $P > 0.1$; Fig. 3A; Table 1). In spring 1996, electrofishing CPE declined to nearly 0. After 4 days of effort, we only captured 23 age-0 largemouth bass. Of these individuals, only 15 were marked, all of which were in the large size class (G-test, $P < 0.05$; Fig. 3B; Table 1). Both energy density and total energy content of the few recaptured, marked largemouth bass fell considerably from fall values (Scheffe's test, $P < 0.05$; Figs. 4A and 4B; Table 2). In fall, large predators were exclusively large largemouth bass (mean length ± 1 SD = 207 ± 39 mm, N = 33); 82% of these largemouth bass had consumed fish on the day we sampled, of which 27% were age-0 largemouth bass. In spring, 71% of largemouth bass predators (287 ± 90 mm, N = 30) consumed fish, although only 3% contained age-0 largemouth bass.

Following stocking of Clark Lake in fall 1995, we captured about 8% fewer small marked largemouth bass than we had stocked a week earlier (G-test, G = 18.9, $P < 0.05$; Fig. 3C). As in Kokosing Lake, CPE of largemouth bass was high at 1.1 largemouth bass/min. As indicated by the high CPE, 12 623 ± 1247 age-0 largemouth bass (Petersen estimate ± 95% CIs) were in Clark Lake, resulting in a higher than anticipated density of 2.8 individuals/m shoreline (resident plus stocked). In spring, CPE fell to 0.2 largemouth bass/min (resident plus stocked individuals), with only 350–490 (modified Schnabel estimate; 95% CI) stocked largemouth bass remaining. Hence, >95% of small (<120 mm) stocked individuals died (Figs. 3C, 3D, and 5A; Table 1). Although mortality was high in Clark Lake, our abundance estimates suggest that more age-0 largemouth bass survived in this system than in Kokosing Lake overwinter. Conversely, survival of large individuals was generally high (Figs. 3C, 3D, and 5A; Table 1). At large sizes, high variance and values exceeding 100% winter survival likely occurred because some individuals grew from their initial fall size classes (Fig. 5A). As in Kokosing Lake, largemouth bass energy density and total energy content declined through winter (Scheffe's test, $P < 0.05$; Figs. 4C and 4D; Table 2). In fall and spring, predators (again exclusively large largemouth bass) were abundant (fall length 272 ± 112 mm, N = 20; spring length 309 ± 39 mm, N = 54), mostly consuming fish (fall diets 75% with fish; spring diets 67% with fish). However, ≤5% of these large predators contained young largemouth bass in fall or spring.

Pond experiments

Unlike reservoirs, similar proportions of small and large individuals survived in Pond Experiment A (N = 4 ponds, Figs. 3E, 3F, and 4B; Table 1). All largemouth bass grew through June (Figs. 3E and 3F), likely by consuming macroinvertebrates and fathead minnow. Apparently, some large (now age 1 year) largemouth bass spawned in May. Hence, small, newly hatched largemouth bass (about 15 mm) also were available as forage in late spring. During pond experi-

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Fig. 3. Proportion of total marked largemouth bass in each 5-mm size class in Ohio (A–D) reservoirs (captured by electrofishing) and (E–H) hatchery ponds (stocked into ponds and then recovered by pond draining) during fall 1995 through spring 1996. Actual proportions of individuals in small classes (open bars) and large classes (solid bars) are given in parentheses.

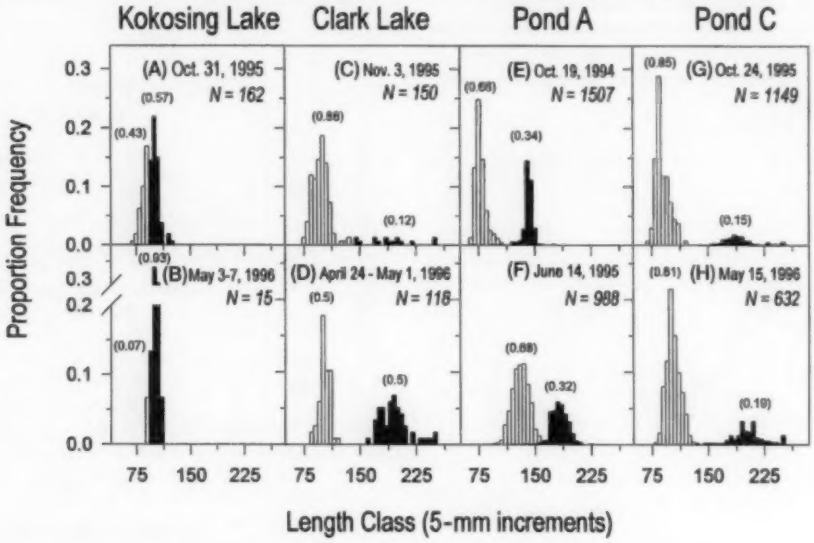

Table 1. Mean ± 1 SD total length (mm) and relative number of marked small and large largemouth bass stocked in fall and recaptured in spring in Ohio reservoirs and hatchery ponds.

Experiment (year)	Experimental unit	Length group	Fall size (±1 SD)	Spring size (±1 SD)	Fall *N*	Spring *N*	*G*	*P*
Reservoir (1995–1996)	Kokosing	Small	88±5	92	3207	1	12.3	<0.001
		Large	103±8	109±21	3401	14		
	Clark	Small	92±9	106±17	7500	59	231.5	<0.001
		Large	195±23	197±22	284	59		
Pond A (1994–1995)	1	Small	80±93	137±5	209	162	3.4	+
		Large	142±6	184±7	105	103		
	2	Small	78±3	122±8	263	130	0.1	ns
		Large	144±7	175±8	135	70		
	3	Small	80±6	141±7	263	191	0.8	ns
		Large	143±5	194±10	136	88		
	4	Small	78±6	130±16	260	188	14.6	<0.001
		Large	142±6	177±7	135	56		
Pond B (1995)[a]	1	Small	132±10	134±10	102	56	2.5	ns
		Large	184±9	180±5	105	76		
	2	Small	131±10	133±14	101	77	0.05	ns
		Large	186±10	186±14	100	79		
Pond C (1995–1996)	1	Small	92	102±11	250	186	1.2	ns
		Large	195	192±20	49	44		
	2	Small	92	105±19	250	58	8.8	<0.01
		Large	195	238±22	25	15		
	3	Small	92	109±9	300	128	9.6	<0.01
		Large	195	218±26	25	23		
	4	Small	92	107±9	200	140	0.2	ns
		Large	195	202±19	50	38		

Note: Pond experiments A and C were designed to explore the effect of size on overwinter success. Pond experiment B assessed our ability to recover small and large largemouth bass within 24 h of stocking. Because largemouth bass in pond experiment C were obtained from the same group stocked into Clark Lake, initial sizes of small and large largemouth bass were the same as those added to Clark Lake. Results of *G*-tests where $P > 0.1$ were not significant (ns) and $0.1 \geq P > 0.05$ were marginally significant (+).

[a]For pond experiment B, fall and spring refer to numbers stocked and numbers recovered 24 h later, respectively.

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Fig. 4. Energy density and total energy content as a function of total length for largemouth bass in (A–D) reservoir, (E and F) pond, and (G and H) pool experiments in fall 1995 and spring 1996. Because all largemouth bass originated from the same group of pond largemouth bass in the fall (Figs. 4E and 4F), we compared their spring energy density and total energy content with this initial distribution. Lines on each panel derive from regression models for kJ/g wet weight = mm total length × 0.0194 + 2.367 (r^2 = 0.33, N = 40) and total kJ = 3.22 × 10^{-6} × $mm^{3.6}$ (r^2 = 0.91, N = 40) for fall largemouth bass (Figs. 4E and 4F). In Figs. 4A–4F, solid circles derive from fall whereas open circles derive from spring. In Figs. 4G and 4H, open squares, triangles, and inverted triangles represent values from high-, low-, and no-ration treatments in spring, respectively. For largemouth bass >125 mm total length, total energy content values were quite high (>4 × 10^4) and are not included in Figs. 4B, 4D, 4F, and 4H. See Table 2 for statistical comparisons and sample sizes.

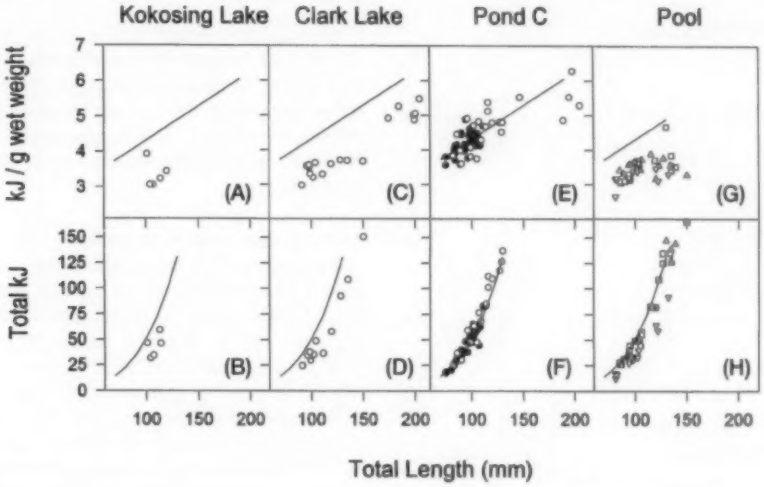

Table 2. Results of Scheffe's multiple comparisons for changes in adjusted mean kJ/g wet weight and total kJ (backcalculated from $\log_e(x)$-transformed data) in multiple-scale experiments during winter 1995–1996.

Experiment	Treatment	N	Change in kJ/g	P	Change in total kJ	P
Reservoir	Kokosing	5	–1.1	<0.05	–19.3	<0.05
	Clark	13	–0.93	<0.05	–10.5	<0.05
Pond C	None	20	0.090	ns	1.5	ns
Pool	High food	15	–0.80	<0.05	–4.2	ns
	Low food	14	–0.95	<0.05	–8.2	<0.05
	No food	12	–0.96	<0.05	–18.1	<0.05

Note: Both ANCOVAs for kJ/g and total kJ were significant (kJ/g: treatment, F = 43.8, df = 6, 111, P < 0.05; length, F = 31.9, df = 1, 111, P < 0.05; total kJ: treatment, F = 35.4, df = 6, 111, P < 0.05; length, F = 1086, df = 1, 111, P < 0.05). Differences between adjusted means are spring minus fall, in which all largemouth bass in experiments originated from the same group of fall individuals. Negative values arise when energy density or total kilojoules declined during winter. Differences between adjusted means overlapping zero were not significant (ns, P > 0.05). Only largemouth bass <125 mm were included in this analysis. See Fig. 4 for graphical presentation.

ment A, we were unable to recapture, on average, about 33% of largemouth bass originally stocked into ponds (Table 1). In pond experiment B, small and large largemouth bass were equally recoverable (G-test, P > 0.05; Table 1). However, we were unable to recover a total of 30% after draining, suggesting that the 33% loss of individuals in pond experiment A likely was unrelated to winter mortality and due to our inability to recapture all individuals during pond draining.

During winter 1995–1996 in pond experiment C, 23–50% of largemouth bass were lost in three ponds whereas 77% were not recovered from pond 2 (Table 1; Figs. 3G and 3H). Retention of both fin clips and spray marks was >99% across all ponds and sizes. More small individuals died than large ones in two (ponds 2 and 3) of four ponds during winter (Fig. 5C; Table 1), although this loss was slight compared with reservoirs. Interestingly, the two ponds (ponds 2 and 3) with high losses of small individuals also had the greatest size disparity between small and large largemouth bass (Table 1; Fig. 5C). Assuming that largemouth bass ≤50% of the length of conspecifics are vulnerable to cannibalism (Johnson and Post 1996), we calculated the proportion of small largemouth bass vulnerable to average-sized (in length, see Table 1) large largemouth bass in each pond. In ponds 2 and 3 in which size-selective mortality occurred, 95 and 77% of small largemouth bass were vulnerable versus only 40 and 43% in ponds 1 and 4 (Fig. 5C). Hence, cannibalism likely contributed to differential mortality in ponds 2 and 3. Without abundant piscine prey and an extended spring in ponds (in contrast, largemouth bass remained in ponds for 1 month longer in pond experiment A), largemouth bass did not grow (Figs. 3G and 3H). Unlike Kokosing and Clark reservoirs, neither largemouth bass energy density nor total energy content changed during winter (Scheffe's test, P < 0.05; Figs. 4E and 4F; Table 2).

Pool experiments

Survival in pools was high; only seven of 90 largemouth bass died. When unfed, largemouth bass consistently lost

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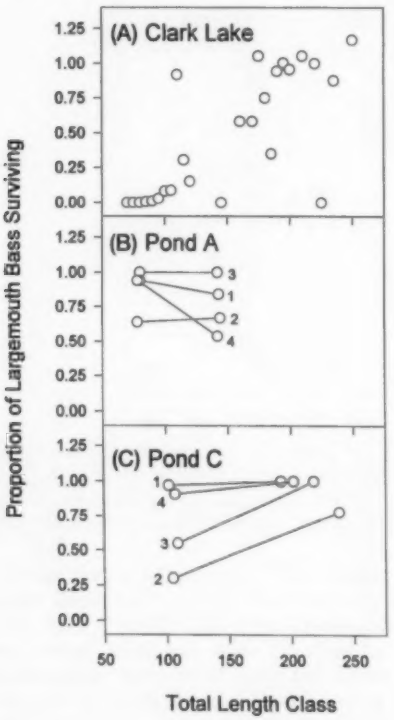
Fig. 5. Proportion of largemouth bass surviving (number in spring/number in fall) as a function of mean total length (mm) per size class in (A) Clark Lake, Ohio, during winter 1995–1996 and (B and C) 0.4-ha hatchery ponds (N = 4 ponds/year), Hebron State Fish Hatchery, during the winters of 1994–1995 and 1995–1996. Numbers correspond to individual ponds (see Table 1). In spring, the number of largemouth bass in ponds was increased by 30% to adjust for individuals lost during pond draining.



wet weight during fall through spring, regardless of length (paired t-test, P = 0.0001, linear regression, not significant; Figs. 6A–6C). In the low-ration treatment, all fathead minnow were consumed each week during fall (October–January) and spring (March–April). Conversely, few fathead minnow were consumed each week during winter (January–March) when temperatures were <6°C (see Fig. 1). During fall, large largemouth bass in this low-ration treatment grew more than small counterparts (linear regression, P = 0.003; Fig. 6D). During winter, largemouth bass of all sizes lost weight (paired t-test, P = 0.0001; Fig. 6E). During spring in this treatment, on average, neither small nor large largemouth bass grew, although growth was quite variable (paired t-test, not significant; Fig. 6F). When fed a high ration, all fathead minnow were not consumed weekly, suggesting that this ration provided an excess of prey. All sizes of these high-ration largemouth bass grew during fall and spring (paired t-test, P = 0.0001, linear regression, not significant; Figs. 6G and 6I) but lost weight during winter, even given a surplus of fathead minnow (paired t-test, P = 0.0001; Fig. 6H). Despite substantial differences in wet weight change across rations, energy densities of largemouth bass consistently declined through winter for largemouth bass regardless of ration (Scheffe's test, $P < 0.05$; Fig. 4G; Table 2). However, total energy content of largemouth bass fed a high ration did not change through winter whereas total energy content declined slightly and severely for largemouth bass with low and no rations, respectively (Fig. 4H; Table 2).

Discussion

During fall through spring, small fall size always reduced survival of largemouth bass in reservoirs but not in ponds and pools, suggesting that slow first-summer growth may not always translate to poor recruitment to older life stages. Below, we explore how temperature, food availability, and predation potentially interacted to drive these patterns of mortality.

Growth and energy reserves

For fishes, high mortality should occur when energy reserves (e.g., lipids) are exhausted during winter starvation (e.g., Oliver et al. 1979; Thompson et al. 1991; Ludsin and DeVries 1997). Because lipids are energy dense (Black 1958), we expected that total energy content and energy density of all starving fish would decline during winter, leading to increased mortality of small fish with low initial energy reserves. As expected, all starved largemouth bass in pools lost considerable weight and total energy content, quite similar to patterns of energy depletion in Kokosing and Clark reservoirs. As such, reservoir largemouth bass likely did not feed during winter. Potentially, starvation occurred in reservoirs because stocking greatly increased largemouth bass densities, increasing intraspecific competition for limited food. Although largemouth bass in both pools and reservoirs were starving, high mortality of small individuals only occurred in reservoirs. Thus, energy depletion of starving individuals probably was not the sole factor contributing to patterns of mortality at the reservoir scale.

Although largemouth bass apparently did not feed in reservoirs during winter, variable food availability among systems might influence patterns of energy depletion. The extent of this food-driven variability in energetic condition might be tempered by winter temperature because largemouth bass and smallmouth bass (*Micropterus dolomieu*) have been suggested to cease feeding at winter temperatures (i.e., <10°C) and thus should lose weight and energy reserves regardless of food availability (e.g., Johnson and Charlton 1960; Shuter et al. 1980). Contradicting this conventional view, largemouth bass in pools containing fathead minnow fed and grew during a much greater proportion of winter than expected, with growth and consumption only ceasing below 6°C. Thus, food availability during winter months likely influences patterns of energy depletion across systems.

During winter, prey ration affected growth, as it certainly does during summer (Garvey et al. 1998). Overwinter in pools with 0.5× ration, largemouth bass slightly increased their wet weight, although surprisingly, both energy density and total energy content declined. With high ration, largemouth bass increased wet weight, even while energy density declined and total energy content remained unchanged.

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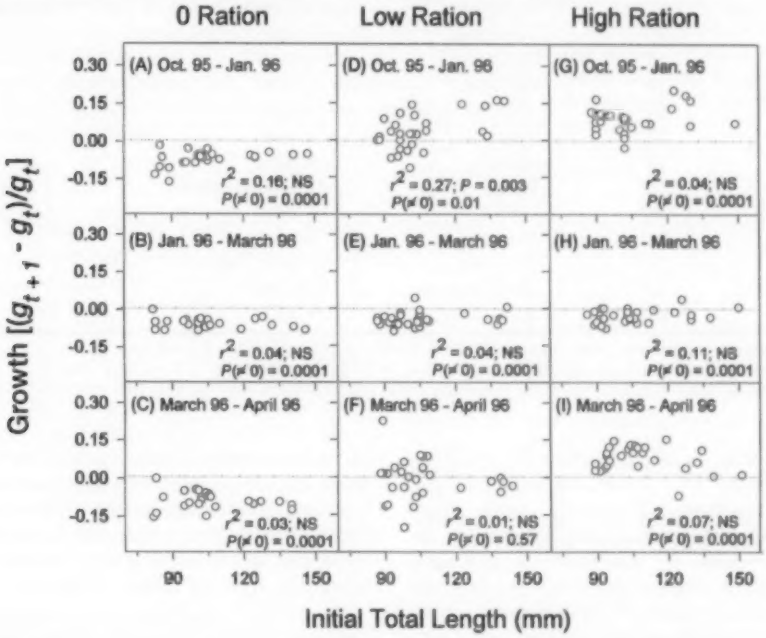
Fig. 6. Growth (change in g wet weight/g wet weight at the beginning of each period) as a function of initial total length for largemouth bass in winter 1995–1996 pool experiments with (A–C) no ration, (D–F) low ration, or (G–I) high ration. Fathead minnow were added to pools each week at either 0.5× (low ration, Figs. 6D–6F) or 1.5× (high ration, 6G–6I) of largemouth bass maintenance ration as calculated via bioenergetics (Hewett and Johnson 1992). Each point represents an individual largemouth bass (N = 25–30/panel). On each panel, results from linear regression of growth as a function of length (top line) and a paired t-test determining if average growth differed from zero (bottom line) are included (for significance, $P \leq 0.006$).



Given these changes, body composition of largemouth bass consuming fathead minnow must have changed during winter, potentially from a high proportion of fat (at 26.3 mg fat/kJ) to a relatively high proportion of protein (at 54.9 mg protein/kJ). To illustrate, assuming that carbohydrates and other body materials remain relatively constant (Weatherley and Gill 1987), a 5-g (dry weight) individual composed of 20% protein and 10% fat will contain the same total energy content (and a higher energy density by dry weight) as a 5.9-g individual composed of 25% protein and 5% fat. Because the proportion of water in tissues increases with declining fat (Niimi 1972), energy density as estimated by kilojoules per gram wet weight should decline even more with increasing protein growth.

In contrast with largemouth bass in pools with fathead minnow, those in ponds without fish prey did not change their weight, energy density, and total energy content during winter. Macroinvertebrates associated with vegetation likely were sufficiently abundant in ponds to allow largemouth bass to maintain weight and energy reserves. Although temperatures in ponds were slightly warmer during winter than in other systems, it is not clear how these warmer temperatures contributed to metabolism, feeding activity, and observed growth. Perhaps differences between the proximate composition of fish prey in pools and macroinvertebrates in ponds influenced allocation patterns and, hence, observed changes in wet weight and energy content. Indeed, proximate composition of prey can dramatically influence protein and fat allocation patterns in cultured fishes (e.g., van Dam and Penning DeVries 1995; Catacutan and Coloso 1995). In summary, growth of feeding largemouth bass during winter was flexible. During fall through spring, actively growing largemouth bass may contain relatively low energy reserves whereas slowly growing fish may be allocating consumed energy toward maintenance of energy reserves. If only one parameter (i.e., length change or energy content) is quantified for either fast-growing or slow-growing fish, one may conclude that condition is poor. Both somatic growth and accumulation of energy reserves must be considered when assessing energetic condition and its potential contribution to survival during winter.

Predation

If starving largemouth bass suffered similar levels of energy depletion across systems, why was mortality only consistently high for small individuals in reservoirs? In our view, energy depletion in concert with predation by large largemouth bass (Miranda and Hubbard 1994*b*) or other species (Green 1982) may have contributed to high mortality of small individuals in reservoirs. For example, although Ludsin and DeVries (1997) documented no size-selective predation in Alabama ponds, they postulated that predation risk may force small largemouth bass into shallow-water refuges with little food during winter (S.A. Ludsin, Ohio State University, 1314 Kinnear Rd., Columbus, OH 43212-1194, U.S.A., personal communication). Extreme fluctuations in water temperature in these shallow areas might be energetically costly, accelerating energy depletion. In reservoirs,

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Table 3. Literature review of studies exploring the role of size on overwinter survival of age-0 largemouth bass.

Source	Latitude	State	Scale of study	Did large age-0 largemouth bass enjoy higher survival?
Ludsin and DeVries 1997	33°	Alabama	6 ponds	Yes[a]
Miranda and Hubbard 1994*a*	34°	Mississippi	1 lake	Yes[a]
Miranda and Hubbard 1994*b*	34°	Mississippi	26 ponds	Sometimes[b]
Adams et al. 1982	36°	Tennessee	1 lake	Yes[a]
Boxrucker 1982	36°	Oklahoma	1 lake	Yes[a]
Shirley and Andrews 1977	36°	Oklahoma	1 lake	No
Aggus and Elliott 1975	37°	Missouri–Arkansas	1 lake	Yes[a]
Chang 1971	38°	Missouri	1 lake	No
Isely 1981	38°	Illinois	5 ponds	No
Kohler et al. 1993	40°	Illinois	2 lakes/6 winters	No
This study	40°	Ohio	4 lakes, 8 ponds, 9 pools	Sometimes[b]
Green 1982	43°	New York	1 lake	Yes[b]
Toneys and Coble 1979	43°	Wisconsin	1 lake, 1 pond	Sometimes[c]
Kolander 1992	45°	South Dakota	2 ponds	No
Wright 1993	46°	Wisconsin	1 lake	No

[a]In these studies, energy depletion due to starvation was implicated as the mechanism underlying differential mortality.
[b]When high mortality of small largemouth bass occurred in these studies, predation was implicated as a potential cause.
[c]In this study, size-selective mortality only occurred at the lake scale, where predators likely were present. Predators were likely absent from the hatchery pond.

small largemouth bass were usually concentrated in shallow water during fall and spring (J.E. Garvey, unpublished data), presumably to avoid predators. Potentially, most small, stocked largemouth bass died in Kokosing Lake either directly through consumption by predators or indirectly through energy depletion in shallow-water refuges. In Clark Lake, in which more small largemouth bass (based on relative CPE) persisted through winter than in Kokosing Lake, direct and indirect effects of predation may have been less intense. Indeed, large largemouth bass consumed mostly non-largemouth-bass prey in fall and spring in Clark Lake.

In ponds and pools, predation was absent, except for two ponds in winter 1995–1996 in which cannibalism may have driven size-selective mortality of small largemouth bass due to the relatively large size disparity between length classes (Johnson and Post 1996). Despite variable food availability in pools and ponds, mortality was generally low and unrelated to size in all other cases. Similarly, in a study exploring how length distributions of fish change through winter, size-selective winter mortality of age-0 largemouth bass occurred in a lake during winter where predators were likely present, but not a in hatchery pond during the same winter (Toneys and Coble 1979). Hence, independently, small fall size may not influence mortality of largemouth bass and perhaps other juvenile fishes during winter. Rather, we hypothesize that predation interacts with fall size and winter food availability to influence growth, survival, and recruitment success (also see Miranda and Hubbard 1994*b*).

Role of body size revisited

At present, most models predicting winter survival of fish are based solely on the interactions among winter energetics, body size, and temperature, assuming that negligible feeding occurs at winter temperatures (Shuter et al. 1980; Gutreuter and Anderson 1985; Lyons 1997). These "classic" models predict that survival of small age-0 fish declines with increasing latitude, implicating starvation during long winters as the causal mechanism. From an evolutionary perspective, these models predict that winter only becomes an important selective force at high latitudes (Conover 1990; Conover and Present 1990). Hence, selection for rapid summer growth of age-0 fish should occur at high latitudes as compensation for short first growing seasons (Conover 1990).

To develop population and evolutionary models for species experiencing a wide range of summer and winter conditions, other important interacting factors should be considered. Our reservoir survey and experiments demonstrated that the effects of fall size on winter survival of age-0 largemouth bass varied across systems under similar winter temperatures and feeding conditions. In addition, the literature revealed that the "classic" model may be incomplete for predicting how first-summer growth influences recruitment (Table 3). In fact, survival of small age-0 largemouth bass relative to large counterparts may generally *increase* with increasing latitude. At low, southern latitudes, relatively high mortality of small age-0 individuals was common, with energy depletion often implicated as the causal mechanism (Table 3). At these low latitudes, the classic model predicts high survival for both small and large individuals because winter starvation should not occur. At higher latitudes across a similar range of lengths to those in southern systems, survival of small and large age-0 largemouth bass often was similar (Table 3), again contradicting model predictions. Interestingly, in systems where the influence of size on winter survival was mixed, predation was the explanatory mechanism suggested (Green 1982; Miranda and Hubbard 1994*b*).

Given our results and the apparently contradictory latitudinal pattern, we must modify current simplistic models. Predation, in concert with energy depletion, might be important when (*i*) winter temperatures are warm and predators are active, as in southern systems (as suggested by Miranda and Hubbard 1994*b*), (*ii*) periods of fall cooling and spring warming are long, as in southern and some middle-latitude systems (this study), or (*iii*) cold-active piscivores (such as

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large percids) are abundant, as in some northern systems (see Green 1982). All of these conditions may increase mortality of age-0 largemouth bass either directly through active predation or indirectly through increased energy depletion in refuges. Hence, the probability of winter survival and recruitment may be increased by improving first-summer growth (e.g., by providing abundant, appropriately sized prey fish as forage), improving factors that facilitate winter survival of small individuals (e.g., by providing winter refuge), and fostering growth during fall, winter, and spring months (e.g., by increasing habitat for macroinvertebrate prey and, thus, their availability).

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References

Adams, S.M., and DeAngelis, D.L. 1987. Indirect effects of early bass–shad interactions on predator population structure and food-web dynamics. *In* Predation: direct and indirect impacts on aquatic communities. *Edited by* W.C. Kerfoot and A. Sih. University Press of New England, Hanover, N.H. pp. 103–117.

Adams, S.M., McLean, R.B., and Huffman, M.M. 1982. Structuring of a predator population through temperature-mediated effects on prey availability. Can. J. Fish. Aquat. Sci. **39**: 1175–1184.

Aggus, L.R., and Elliott, G.V. 1975. Effects of cover and food on year-class strength of largemouth bass. *In* Black bass biology and management. *Edited by* H. Clepper. Sportfishing Institute, Washington D.C. pp. 317–322.

Black, E.C. 1958. Energy stores and metabolism in relation to muscular activity in fishes. *In* The investigation of fish-power problems. *Edited by* P.A. Larkin. University of British Columbia, Vancouver, B.C.

Boxrucker, J. 1982. First year growth and survival of stocked largemouth bass in a small Oklahoma impoundment. Proc. Annu. Conf. Southeast. Assoc. Fish Wild. Agencies, **36**: 369–376.

Bremigan, M.T., and Stein, R.A. 1994. Predator gape and zooplankton size: exploring a size-dependent recruitment mechanism in fishes. Can. J. Fish. Aquat. Sci. **51**: 913–922.

Cargnelli, L.M., and Gross, M.R. 1996. The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). Can. J. Fish. Aquat. Sci. **53**: 360–367.

Catacutan, M.R., and Coloso, R.M. 1995. Effect of dietary protein to energy ratios on growth, survival, and body composition of juvenile Asian seabass, *Lates calcarifer*. Aquaculture, **131**: 125–133.

Chang, K.B. 1971. Population characteristics of largemouth bass and bluegill in a Missouri pond with an evaluation of some sampling methods. M.A. thesis, University of Missouri, Columbia, Mo.

Christensen, B. 1996. Predator foraging capabilities and prey antipredator behaviours: pre- versus postcapture constraints on size-dependent predator–prey interactions. Oikos, **76**: 368–380.

Conover, D.O. 1990. The relation between capacity for growth and length of growing season: evidence for and implications of countergradient variation. Trans. Am. Fish. Soc. **119**: 416–430.

Conover, D.O., and Present, T.M.C. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. Oecologia, **83**: 316–324.

Feinberg, S.E. 1980. The analysis of cross-classified categorical data. The MIT Press, Cambridge, Mass.

Garvey, J.E., and Stein, R.A. 1998. Linking bluegill and gizzard shad prey assemblages to growth of age-0 largemouth bass in reservoirs. Trans. Am. Fish. Soc. **127**: 70–83.

Garvey, J.E., Dingledine, N.A., Donovan, N.S., and Stein, R.A. 1998. Exploring spatial and temporal variation within reservoir food webs: predictions for fish assemblages. Ecol. Appl. **8**: 104–120.

Green, D.M. 1982. Population dynamics of largemouth bass (*Micropterus salmoides*) and chain pickerel (*Esox niger*) in Dryden Lake, New York. Ph.D. dissertation, Cornell University, Ithaca, N.Y.

Gutreuter, S.J., and Anderson, R.O. 1985. Importance of body size to the recruitment process in largemouth bass. Trans. Am. Fish. Soc. **114**: 317–327.

Hambright, K.D., Drenner, R.W., McComas, S.R., and Hairston, N.G., Jr. 1991. Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. Arch. Hydrobiol. **121**: 389–404.

Hewett, S.W., and Johnson, B.L. 1992. Fish bioenergetics model 2, an upgrade of a generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, Madison, Wis.

Holland-Bartels, L.E., Littlejohn, S.K., and Huston, M.L. 1990. A guide to the larval fishes of the upper Mississippi River. U.S. Fish and Wildlife Service, LaCrosse, Wis.

Isely, J.J. 1981. Effects of water temperature and energy reserves on overwinter mortality of young-of-year largemouth bass (*Micropterus salmoides*). M.S. thesis, Southern Illinois University, Carbondale, Ill.

Johnson, M.G., and Charlton, W.H. 1960. Some effects of temperature on the metabolism and activity of the largemouth bass, *Micropterus salmoides*, Lacepede. Prog. Fish-Cult. **22**: 155–163.

Johnson, J.M., and Post, D.M. 1996. Morphological constraints on intracohort cannibalism in age-0 largemouth bass. Trans. Am. Fish. Soc. **125**: 809–812.

Kohler, C.C., Sheehan, R.J., and Sweatman, J.J. 1993. Largemouth bass hatching success and first-winter survival in two Illinois reservoirs. N. Am. J. Fish. Manage. **13**: 125–133.

Kolander, T.D. 1992. Factors limiting overwinter survival of young-of-the-year largemouth bass in South Dakota. M.S. thesis, South Dakota State University, Brookings, S.D.

Ludsin, S.A., and DeVries, D.R. 1997. Understanding first-year survival of a freshwater piscivore: the inter-dependency of life-history stages. Ecol. Appl. **7**: 1024–1038.

Lyons, J. 1997. Influence of winter starvation on the distribution of smallmouth bass among Wisconsin streams: a bioenergetics modeling assessment. Trans. Am. Fish. Soc. **126**: 157–162.

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May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. The early life history of fishes. Springer-Verlag, New York.

Miller, R.P. 1981. Simultaneous statistical inference. 2nd ed. Springer Verlag, New York.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**: 1657–1670.

Miranda, L.E., and Hubbard, W.D. 1994*a*. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Trans. Am. Fish. Soc. **123**: 80–87.

Miranda, L.E., and Hubbard, W.D. 1994*b*. Winter survival of age-0 largemouth bass relative to size, predators and shelter. N. Am. J. Fish. Manage. **14**: 790–796.

Neter, J., Wasserman, W., and Kutner, M.H. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. Irwin, Boston, Mass.

Nielsen, L.A. 1992. Methods of marking fish and shellfish. Am. Fish. Soc. Spec. Publ. No. 23.

Niimi, A.J. 1972. Changes in the proximate body composition of largemouth bass (*Micropterus salmoides*) with starvation. Can. J. Zool. **50**: 815–819.

Oliver, J.D., Holeton, G.F., and Chua, K.E. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Trans. Am. Fish. Soc. **108**: 130–136.

Post, J.R., and Evans, D.O. 1989. Size-dependent overwinter mortality of young-of-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. **46**: 1958–1968.

Rand, P.S., Lantry, B.F., O'Gorman, R., Owens, R.W., and Stewart, D.J. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for salmonine energetics. Trans. Am. Fish. Soc. **123**: 519–534.

Rice, J.A., Crowder, L.B., and Binkowski, F.P. 1987. Evaluating potential sources of mortality for larval bloater (*Coregonus hoyi*): starvation and vulnerability to predation. Can. J. Fish. Aquat. Sci. **44**: 467–472.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

SAS Institute, Inc. 1985. SAS users guide: statistics. Version 5 edition. SAS Institute Inc., Cary, N.C.

Schael, D.M., Rudstam, L.G., and Post, J.R. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatis*). Can. J. Fish. Aquat. Sci. **48**: 1919–1925.

Seaburg, 1957. A stomach sampler for live fish. Prog. Fish-Cult. **19**: 137–139.

Shirley, K.E., and Andrews, A.K. 1977. Growth, production, and mortality of largemouth bass during the first year of life in Lake Carl Blackwell, Oklahoma. Trans. Am. Fish. Soc. **106**: 590–595.

Shuter, B.J., MacLean, J.A., Fry, F.E.J., and Regier, H.A. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. Fish. Soc. **109**: 1–34.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

Thompson, J.M., Bergarson, E.P., Carlson, C.A., and Keading, L.R. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. Trans. Am. Fish. Soc. **120**: 346–353.

Toneys, M.L., and Coble, D.W. 1979. Size-related, first winter mortality of freshwater fishes. Trans. Am. Fish. Soc. **108**: 415–419.

van Dam, A.A., and Penning DeVries, F.W.T. 1995. Parameterization and calibration of a model to simulate effects of feeding level and feed composition on growth of *Oreochromis niloticus* (L.) and *Oncorhynchus mykiss* (Walbaum). Aq. Res. **26**: 415–425.

Weatherley, A.H., and Gill, H.S. 1987. The biology of fish growth. Academic Press, New York.

Wright, R.A. 1993. Size dependence of growth, consumption, and survival in juvenile largemouth bass: combining experimental manipulation and individual-based simulation. Ph.D. dissertation, University of Wisconsin, Madison, Wis.

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Colonization by lentic macroinvertebrates: evaluating colonization processes using artificial substrates and appraising applicability of the technique

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Abstract: Our objectives were to describe the patterns of colonization of lentic macroinvertebrates on artificial substrates and to evaluate how this information can then be used to effectively and efficiently sample macroinvertebrates in vegetated littoral zones of lakes. Colonization of taxa in terms of both richness and density generally followed a Michaelis–Menton saturating curve with an initially rapid increase in densities up to a plateau within a short period of time (<8 days). We propose that this initial colonization is due to random encounters with the substrate and that the plateau represents a balance between immigration and emigration. Accordance with the saturating colonization curve improved with increasing densities of individuals. As a whole, the spatial pattern of colonization by orders of macroinvertebrates became more aggregated with time, indicating that true random encounter colonization occurs mainly in the early stages, and consequently, this is the time when sampling should best represent relative abundance. In addition, we found that invertebrate colonists of the substrata were concordant with prey items in the guts of rainbow trout (*Oncorhynchus mykiss*), a facultative benthivore.

Résumé : Nous avions pour objectifs de décrire les modalités de colonisation de substrats artificiels par des macroinvertébrés lentiques, et d'établir comment cette information peut être utilisée pour échantillonner efficacement les macroinvertébrés des zones riveraines végétalisées des lacs. La colonisation par les taxons en termes de diversité et de densité suivait généralement une courbe de saturation de Michaelis–Menton, avec un accroissement initial rapide des densités jusqu'à un plateau atteint après une courte période (moins de 8 jours). Nous pensons que cette colonisation initiale est tributaire de contacts aléatoires avec le substrat, et que le plateau reflète un équilibre entre l'immigration et l'émigration. La conformité à la courbe de saturation de la colonisation augmente raison directe de l'accroissement des densités des organismes. Globalement, le profil spatial de colonisation par les ordres de macroinvertébrés devient avec le temps une dispersion agrégative, ce qui montre que la colonisation par contacts aléatoires véritables se produit principalement dans les premiers stades; cette période est donc celle où l'échantillonnage devrait le mieux représenter l'abondance relative. De plus, nous avons observé que les colonisateurs invertébrés du substrat correspondaient aux proies recueillies dans les estomacs de truites arc-en-ciel (*Oncorhynchus mykiss*), des benthivores facultatifs.

[Traduit par la Rédaction]

Introduction

The study of colonization of substrates by freshwater macroinvertebrates has been important in examining the composition and distribution of benthic communities (Minshall and Petersen 1985; Peckarsky 1986; Mackay 1992). Another emphasis of such colonization studies has been on the suitability of artificial substrates for sampling macroinvertebrates in order to estimate richness, abundance, and biomass (Rosenberg and Resh 1982; Suren 1991).

Although numerous studies of the colonization patterns of lotic macroinvertebrates exist (e.g., Doeg et al. 1989*a*, 1989*b*; Giller and Cambell 1989; Boothroyd and Dickie 1991), a thorough treatment of these processes in lentic systems is lacking (e.g., Francis and Kane 1995; Oertli and Lachavanne 1995). Patterns in lentic systems cannot be simply extrapolated from lotic ones, as colonization processes in streams are influenced by drift (Minshall and Petersen 1985; Mackay 1992) and stream benthos tends to be more spatially aggregated at higher densities (Downing 1979; Morin 1985). Colonization of lentic macroinvertebrates on macrophytes has received little attention because sampling epiphytic invertebrates can be problematic, as samplers can be difficult to use and may lack both precision and accuracy (Downing and Cyr 1985). Downing and Cyr (1985) recommended manual removal of macrophytes from quadrats as being most accurate, but this method is extremely time consuming and requires correction for variation in total colonizable surface (i.e., leaf) area among samples. Artificial substrates,

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with a fixed coverage and colonizable surface area, may prove to be an efficient and accurate sampling method.

Rosenberg and Resh (1982) reviewed the benefits and disadvantages of using artificial substrates in the study of macroinvertebrates. Such samplers permit researchers to collect data from habitats that are difficult to accurately sample by conventional methods and may improve the statistical precision of estimates of benthic abundance (Rosenberg and Resh 1982; but see Morin 1985; Boothroyd and Dickie 1989), which can have high levels of uncertainty owing to the contagious distribution of organisms (Elliott 1977; Downing 1979). Increased sampling precision arises from constructing artificial substrates that have identical colonizable areas and also by reducing error accruing as a result of variation in experimenter effort and microhabitat characteristics (depth, substrate quality, etc.).

However, estimates of benthic abundance using artificial substrates may suffer from a trade-off between precision and accuracy (Rosenberg and Resh 1982; Morin 1987; Boothroyd and Dickie 1989; Francis and Kane 1995). The "passive" nature of artificial substrates (i.e., sampling only the animals "attracted" by them) may cause them to be selective in the organisms that they collect (Dudley 1988; Mackay 1992; Oertli and Lachavanne 1995). Furthermore, the rate of colonization will depend on the mobility of individual taxa (Townsend and Hildrew 1976; Giller and Cambell 1989; Oertli and Lachavanne 1995). One way of assessing the accuracy of samplers is to compare the densities on the sampler after a period of time with those found on natural vegetation. Unfortunately, natural vegetation may differ in colonizable surface area, quality, and "succession" stage of colonization, all of which may also affect accuracy. We propose that accuracy of the sampling technique can be evaluated by comparing the colonization pattern on the substrates with that predicted by random encounter colonization theory implicit in Michaelis–Menton saturation curves (Edelstein-Keshet 1988).

The objectives of this study were to (*i*) develop an artificial substrate for lentic systems that minimizes the shortcomings presented in the review by Rosenberg and Resh (1982), (*ii*) quantify the temporal pattern of colonization of an artificial substrate by lentic epiphytic macroinvertebrates and compare these patterns with those expected under random encounter colonization, and (*iii*) assess the ability of the artificial substrate sampler to estimate the prey availability of a facultative benthivorous fish, rainbow trout (*Oncorhynchus mykiss*).

Methods and materials

Artificial substrate sampler

Artificial substrate samplers were constructed from 210 × 210 mm ceramic tiles upon which plastic aquarium plants, designed to mimic the macrophyte foxtail (*Myriophyllum* sp.), were glued. To each tile, nine long (18 cm) and three short (9 cm) fronds were affixed. As the fronds are identical in surface area for a given length, this allowed for consistency of colonizable area among samplers. We minimized the loss of individuals during the collection of the samplers by designing a plexiglass retrieval box that encloses the colonizing community during retrieval. The box was bottomless so that it could be laid on the tiles, and a lip on the inside sealed in the contents. A circular opening covered with 500-μm screen on the top of the box allowed water to drain upon retrieval. The tile could then be washed directly into the box.

Colonization experiment

Colonization experiments were conducted in two small lakes, Crater Pothole 3 (CPH3) and Crater Pothole 4 (CPH4), in south-central British Columbia, Canada (49°56′15″N, 120°33′50″W), during July and August 1992. The lakes are morphometrically similar (3.3 and 5.4 ha surface area and 9.3 and 7.2 m average depth, respectively) and are located within 50 m of one another but are not connected. A more complete description of the study lakes is available in Post et al. (1999). They differed in their densities of the facultative benthivore rainbow trout. CPH3 had about 11 000 age-0 fish/ha and 300 age-1 fish/ha whereas CPH4 (low fish density) possessed 500 age-0 fish/ha and 150 age-1 fish/ha. Such differences in top predator abundance between lakes were used to try to create a wider range of densities of macroinvertebrates with which to examine the colonization process.

Forty-eight artificial substrates were set in each lake in a strip along the shore at 0.75 m depth to match the distribution of natural macrophytes. A randomized block design was used where substrates were placed in 12 groups of four (with 1 m between substrates in a group) with 5 m separating each group. On each sampling day (days 1, 2, 4, and 8), one artificial substrate was removed randomly from each group of four substrates and processed. Experiments in CPH4 were started on July 20, 1992 (and 12 artificial substrates were removed on July 21, 22, 24, and 28), whereas experiments in CPH3 began on August 17, 1992 (substrates removed on August 18, 19, 21, and 25). Although the effect of time might confound the effect of differences between lakes, the goal here was not to compare lakes, but to evaluate the colonization process as thoroughly as possible.

Substrates were gently laid on the lake bottom by divers so as to minimize sediment disruption. The use of the plexiglass box for collection minimized the effect of escaping colonists. Invertebrates were generally found on the macrophyte portion of the sampler, although some were seen on the upper surface of the tiles (e.g., *Gammarus lacustris*). No attempt was made to quantify these two fractions separately. Once collected, samples were stored in 70% ethanol in glass jars and were later identified (to family or genus) and enumerated. Statistical analyses were performed at several levels of taxonomic resolution, including the total macroinvertebrate community density and densities (and richness) by order, family/genus, and functional feeding group (Merritt and Cummins 1984).

Density and taxonomic richness data, for each lake, were fitted to a Michaelis–Menton saturating function (Edelstein-Keshet 1988) of the form

$$\text{Density}\ (i) = \frac{b_0 \times \text{time}_i}{b_1 + \text{time}_i}$$

where density(i) is the number of individuals or number of taxa present on the artificial substrate at time$_i$, b_0 is the equilibrium or saturation density, and b_1 is the time at half saturation (i.e., the time at which density = $0.5b_0$). The function was fitted by nonlinear least squares regression using the NONLIN function in SYSTAT (Wilkinson 1992). Robustness of parameter fits (global versus local solutions) was tested by varying initial parameter values required by NONLIN to fit the curves. Estimates of the parameters b_0 and b_1 along with their confidence intervals, as well as an R^2 value (representing the proportion of the variance in the data that is explained by the model), were used for hypothesis tests.

Allan (1984) proposed that invertebrate densities of much less than five individuals per sampler are too difficult to evaluate quantitatively due to lack of precision. For the purpose of this study, only taxa with mean densities of three or more individuals per sampler at the fourth day of sampling are included.

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Macroinvertebrate abundance and fish diets

Identifying and quantifying the food available to benthivorous fish can be problematic, as they select only the larger and more mobile fraction of benthic invertebrates (Konkle et al. 1990). We hypothesized that our samplers, which mimic natural macrophytes, would be a reasonable method of estimating the relative abundance of large mobile benthic organisms, and consequently, we examined the mutual selectivity of foraging fish and the samplers (i.e., the taxonomic overlap).

Diet data of juvenile rainbow trout (age-1) were collected from CPH3 and CPH4 plus four other similar lakes (CPH1, CPH2, Bluey Pothole 1 (BPH1), and Bluey Pothole 2 (BPH2)) in the area to contrast with benthic community composition and abundance found on the artificial samplers in 1992–1993. A more complete description of the study lakes and details of fish diet sampling and fish spatial distribution is available in Post et al. (1999). Fish were captured by nylon gill nets set in the littoral zone, midshore zone (1.5–2.5 m depths), and pelagic zone of each lake for one to three 1-h periods as necessary to capture a minimum of 30 rainbow trout. Once captured, fish were frozen and brought to the laboratory where they were thawed and dissected for stomach content analysis. Diet items including zooplankton and benthic macroinvertebrates were identified to taxonomic orders and enumerated. Stomach contents of a random sample of 10 fish per habitat (or fewer if <10 were caught to a minimum of three) were pooled and stored in 70% ethanol. Only lake–date combinations with >14 fish across all habitats are included in the analysis. For the purpose of this study, the diet of juvenile rainbow trout was determined for the average fish in the lake on each date sampled by taking a weighted (by the number of fish caught per habitat) arithmetic average diet across the three habitats sampled. The diet of the average fish rather than a habitat-specific diet was used to compare with samplers set in the littoral zone, as fish in these small lakes are known to move into and out of the littoral zone with relatively high frequency (J.R. Post, personal observations).

The macroinvertebrate community composition data included in this section were collected independently from those included in the colonization experiment. Twelve artificial substrates per lake were set for 4 days (see results of the colonization experiment for justification of this duration) at each date at a depth of 0.7–1.0 m at random locations around the lake. Invertebrates were stored in 70% ethanol and later identified to order and enumerated. Only diet samples in which benthos contributed more than 50% of the mass of the stomach contents are included, yielding 10 data sets of a potential 22 different lake–date sets collected during the study. Percent overlap between substrates and diets was calculated using proportional contribution by mass of each taxon in the diet of the average fish (n = 14–30) and on the average artificial substrate (n = 12) for each of the 10 data sets that met the above criterion. Total mass of a taxon within a sample was calculated by taking the average weight of 30 individuals of each taxon within that sample and multiplying it by the density of individuals. Overlap in benthic community composition between artificial substrates and fish stomachs was calculated using Schoener's percent overlap index (Krebs 1989):

$$P_{sd} = \left[\sum^{n} (\text{minimum } p_{is}, p_{id}) \right] 100$$

where P_{sd} is the percent overlap in macroinvertebrate community composition between artificial substrates (s) and fish diets (d), p_{is} and p_{id} are the proportions of the total invertebrate community taken up by taxa i on substrates and in diets by mass, and n is the total number of invertebrate taxa. The index ranges from zero (no overlap) to 100% (complete overlap).

Results

The taxonomic richness measured at the level of orders and families/genera (referred to as genera hereafter) on the artificial substrates rapidly reached an asymptote in both lakes (Fig. 1), with similar values for asymptote in both lakes (Table 1). Both levels of taxonomic resolution produced very similar results for rate of colonization, where taxa colonized artificial substrates in CPH3 almost twice as fast as in CPH4, although the difference was not significant. The fit of the nonlinear model was very good with 92–97% of the variance in the data explained by the model (Table 1).

Cumulative richness plots (i.e., the proportion of the total richness at each time interval) are a graphical method of assessing the rate of species accumulation and a means of assessing the time it takes to capture all potential colonists. These showed that the rate decreased rapidly through time to an asymptote (Fig. 1) for both lakes and levels of taxonomic resolution. For taxonomic orders, the number of taxa on artificial substrates in CPH4 reached an asymptote rapidly (within 2 days), while in CPH3 the number of orders on the artificial substrates increased rapidly during the first day, followed by a much slower rate thereafter. For genera, the pattern of accumulation of taxa was similar, but slower than for orders.

Total number of invertebrates on the artificial substrates showed a very good fit to the saturation model in both lakes (Fig. 2) and explained 90% (CPH3) and 85% (CPH4) of the variance in densities, respectively (Table 2). Saturation densities as well as the rate of colonization did not differ significantly between lakes.

Analyses at the taxonomic level of order produced a range in R^2 values from 0.53 to 0.84 (Table 2; Fig. 2). In both lakes, Diptera, Amphipoda, Tricladida (Turbellaria), Ephemeroptera, and Mesogastropoda accounted for >90% of all individuals collected (Table 2). In general, CPH3 (high fish density) had higher densities of these taxa as compared with CPH4, with the exception of Amphipoda, and CPH3 had a much more equitable distribution of taxa. Times to half saturation varied among orders (range 1.11–16.62 days in CPH3 and 0.30–9.48 days in CPH4).

Most taxa when grouped by the lowest taxonomic resolution (family or genus) were not dense enough to warrant inclusion in the analyses. Of those taxa that were dense enough to be included on their own, *Dugesia* sp. (Turbellaria), *Gammarus lacustris* (Amphipoda), Chironomidae, Ephydridae, and Baetidae dominated the community on the substrates in CPH3 (Table 2). In CPH4, artificial substrates were strongly dominated by *Gammarus lacustris*, with high densities of the turbellarian *Dugesia* sp., followed by lower densities of Baetidae and *Limnea truncatula* (Mesogastropoda). Time to half saturation was highly variable between lakes and ranged from 1.43 to 90.98 days in CPH3 and from –0.16 (i.e., departure of individuals later on) to 9.5 days in CPH4. Note that the estimate of 91 days in CPH3 was accompanied by very large confidence intervals, resulting from a continued increase in chironomid density by the end of the experiment (i.e., value of asymptote is uncertain).

Analyses using functional feeding groups were performed to determine the importance of biological interactions in early colonization (Oertli and Lachavanne 1995). Coloniza-

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Fig. 1. Taxonomic richness for data organized by order and family (or genus when possible). Upper panels are plots of mean (±95% CI) number of taxa over time, fitted using the saturating function. Lower plots show the cumulative proportion of the total number of taxa found on the 12 samplers on each sampling date. CHP3: solid lines and circles; CPH4: dotted lines and triangles.

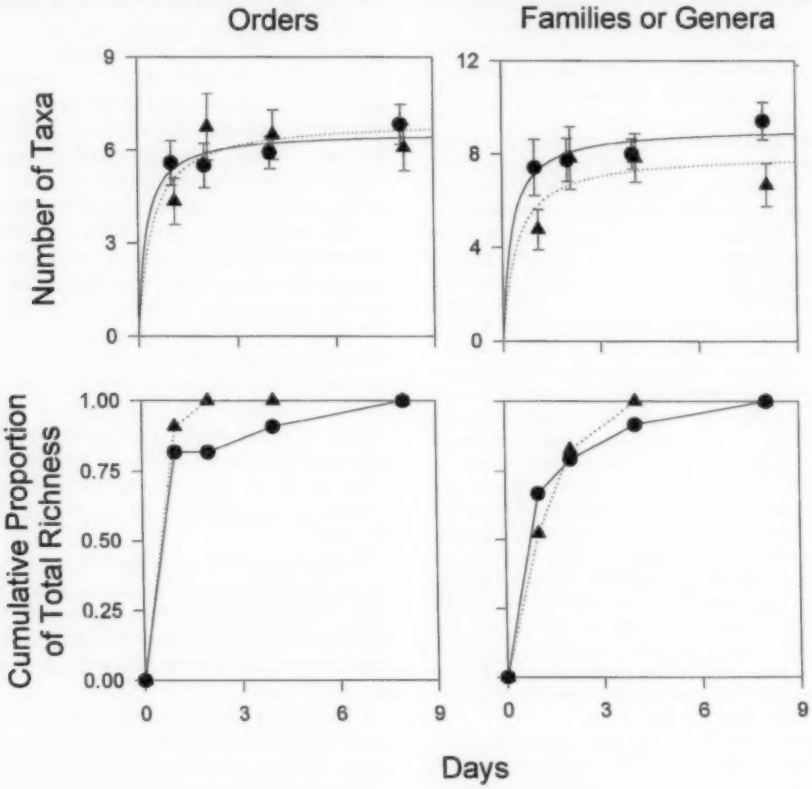

Table 1. Parameter estimates and assessment of the fit of the saturating curve for richness (number of taxa) at the level of orders and families (or genera when possible) on artificial substrates (n = 48).

	R^2	Saturation density (b_0) (mean ± 95% CI)	Time at half saturation (b_1) (mean ± 95% CI)
Orders			
CHP3 (high fish density)	0.97	6.59 (5.90, 7.28)	0.24 (0, 0.48)
CHP4 (low fish density)	0.94	6.98 (6.04, 7.92)	0.41 (0.07, 0.76)
Genera			
CHP3 (high fish density)	0.96	9.15 (8.18, 10.13)	0.28 (0.03, 0.53)
CHP4 (low fish density)	0.92	8.05 (6.85, 9.25)	0.43 (0.05, 0.82)

tion patterns generally agreed with the colonization model (Fig. 3), with a high R^2 in most groups (Table 3). Communities on substrata from both lakes were dominated by predators, scrapers, and collectors. Times to half saturation were relatively short (range 1.5–10.8 days in CPH3 and 0.5–5.1 days in CPH4).

For each taxon, aggregation indices (variance to mean ratios) were calculated for each time interval, and a linear regression then performed to test if these ratios varied significantly with time. The majority of taxa did become increasingly spatially aggregated over time, but this pattern was significant in only a few instances, as sample sizes (n = 4) for each regression were low (Tables 2 and 3). As a result, an average aggregation index (over all sampling days) was calculated for each taxon and compared with a chi-square distribution to test if the distribution of organisms was random (Elliott 1977). All but shredders in CPH3 showed a significantly aggregated pattern.

The mean and variance in density of each order and sampling day were pooled across sampling days and a $\log_{10}$–$\log_{10}$ regression of variance on mean (an index of aggregation) was performed for each day (i.e., all orders at day 1 pooled together; same for days 2, 4, and 8). Data from the two lakes were pooled to increase sample size. The analyses

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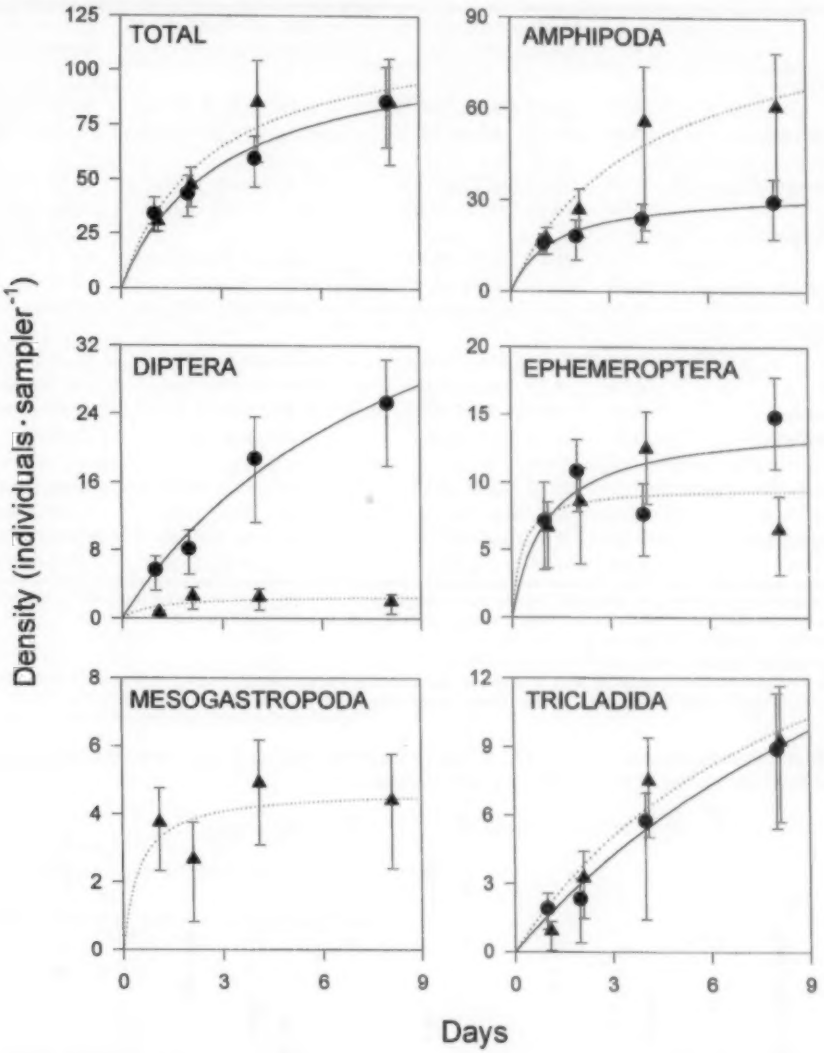
Fig. 2. Total density and densities of macroinvertebrates (mean ± 95% CI) in each order over time, fitted using the saturating function. CHP3: solid lines and circles; CPH4: dotted lines and triangles.



showed that slope increased over time, although only the slope at day 1 was significantly different from that of day 8 (ANCOVA, $p = 0.0014$) (Table 4). Initially, the slope increases rapidly, with the rate of change decreasing over time. On day 1, the slope ($b = 1.051$) did not differ from that of a random distribution of individuals ($b = 1$) (t-test, $p > 0.05$). Thus, aggregation increases most rapidly (from an initially random distribution) early on during colonization.

Across orders (and including total densities), a correlation using $\log_{10}(x + 1)$-transformed data showed that the R^2 values of the nonlinear fittings increased significantly ($p = 0.047$) with the predicted asymptotic density of organisms (Fig. 4). Thus, variation in fit of the model was explained in part (Pearson correlation coefficient $r = 0.61$) by the density of colonists.

We calculated a mean time to half saturation (b_1) for each lake and for all levels of taxonomic organization using only taxa with positive values for mean time to half saturation (negative times indicate that the model is inappropriate as values decrease after a peak during the sampling period) (Table 5). In general, mean estimates (range 2.83–7.02 days) were similar between lakes and among levels of organization, and the overall mean time to half saturation across all levels of organization was 4.09 days. This overall mean falls within or above the confidence limits of estimates of mean time to half saturation for all the individual taxa/groupings considered here.

Macroinvertebrate abundance and benthivorous fish diets

Overlap in species composition and abundance on artificial substrate samplers and trout diet composition was vari-

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Table 2. Parameter estimates and assessment of the fit and suitability of the saturating curve for densities of individuals on artificial substrates.

	R^2	Saturation density (b_0) (mean ± 95% CI)	Time at half saturation (b_1) (mean ± 95% CI)	Density at day 4 (mean ± 95% CI)	s^2/x (mean)
CHP3 (high fish density)					
Total invertebrates	0.90	114.03 (78.31, 149.75)	3.03 (0.77, 5.28)	59.67 (46.43, 69.79)	6.28[a,c]
Tricladida (Turbellaria: *Dugesia* sp.)	0.60	27.67 (–33.44, 88.79)	16.62 (–33.51, 66.75)	5.75 (1.426, 6.99)	4.06[a,b]
Amphipoda (*Gammarus lacustris*)	0.79	33.64 (21.53, 45.74)	1.43 (–0.24, 3.10)	23.83 (16.18, 28.86)	5.77[a,c]
Ephemeroptera	0.84	14.53 (10.25, 18.80)	1.11 (–0.09, 2.31)	7.67 (4.57, 9.94)	1.61[a,b]
Baetidae (early instar)	nc			4.64 (3.06, 6.83)	1.85[a,b]
Diptera	0.81	54.64 (12.52, 96.77)	8.91 (–2.20, 20.03)	18.75 (11.25, 23.64)	3.71[a,b]
Chironomidae	0.79	206.27 (–1299.16, 1711.71)	90.98 (–622.10, 804.05)	7.77 (5.91, 10.13)	2.64[a,b]
Ephydridae	0.67	13.93 (6.19, 21.68)	3.36 (–0.79, 7.51)	7.54 (3.77, 14.28)	3.08[a,b]
CHP4 (low fish density)					
Total invertebrates	0.85	121.51 (82.61, 160.41)	2.63 (0.55, 4.71)	85.25 (57.99, 104.43)	9.90[a,d]
Mesogastropoda	0.74	4.72 (3.05, 6.39)	0.47 (–0.53, 1.46)	4.92 (3.09, 6.18)	1.44[a,b]
Limnea truncatula	0.69	3.84 (2.36, 5.33)	0.30 (–0.65, 1.26)	3.52 (2.35, 5.10)	1.55[a,b]
Tricladida (Turbellaria: *Dugesia* sp.)	0.79	21.11 (4.31,37.90)	9.48 (–2.47,21.43)	7.50 (5.03, 9.38)	1.93[a,b]
Amphipoda (*Gammarus lacustris*)	0.70	97.35 (37.83, 156.88)	4.16 (–1.13, 9.46)	55.83 (19.91, 73.83)	16.03[a,b]
Ephemeroptera	0.69	9.69 (6.47, 12.91)	0.30 (–0.46, 1.06)	12.50 (8.40, 15.23)	3.42[a]
Baetidae (early instar)	0.29	1.21 (0.30, 2.11)	–0.16 (–1.17, 0.84)	10.03 (7.65, 13.07)	3.28[a]
Diptera	0.53	2.76 (1.39, 4.14)	1.03 (–0.78, 2.83)	2.98 (0.99, 3.47)	2.60[a]

Note: Analysis is presented for three levels of taxonomic organization (in each case, $n = 48$). Only taxa with mean day 4 densities of three or more individuals are included. nc, nonconvergence of nonlinear model because mean density decreased after day 2.

[a]Significantly different from a random distribution (χ^2, $p < 0.05$).

[b]Degree of spatial aggregation increases with time (but is not significant).

[c]Distribution becomes significantly more contagious with time (linear regression, $n = 4$, $p < 0.05$).

[d]Distribution becomes significantly more contagious with time (linear regression, $n = 4$, $p < 0.10$).

Fig. 3. Densities of macroinvertebrates (mean ± 95% CI) in various functional feeding groups over time, fitted using the saturating function. CHP3: solid lines and circles; CPH4: dotted lines and triangles.

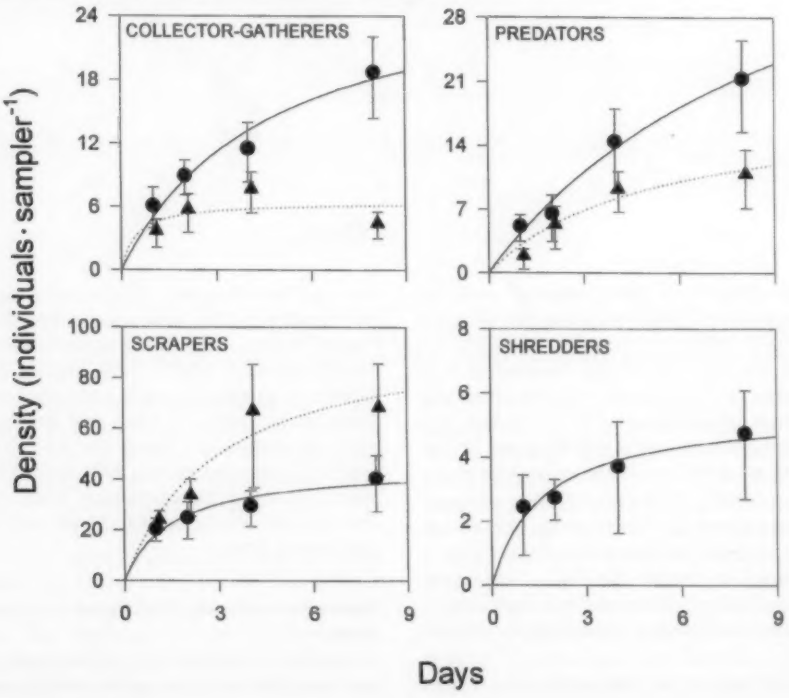

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Table 3. Parameter estimates and assessment of the fit and suitability of the saturating curve for densities of individuals on artificial substrates.

	R^2	Saturation density (b_0) (mean ± 95% CI)	Time at half saturation (b_1) (mean ± 95% CI)	Density at day 4 (mean ± 95% CI)	s^2/x (mean)
CHP3 (high fish density)					
Collector–gatherers	0.88	28.78 (16.43, 41.13)	4.74 (0.65, 8.83)	11.55 (8.34, 13.94)	1.52[a,b]
Predators	0.82	50.51 (5.09, 95.93)	10.76 (–4.05, 25.58)	14.45 (9.89, 18.00)	3.08[a,b]
Scrapers	0.84	45.51 (31.35, 59.67)	1.51 (0.01, 3.00)	29.78 (21.48, 35.60)	5.39[a,c]
Shredders	0.73	5.49 (3.04, 7.93)	1.62 (–0.60, 3.83)	3.73 (1.61, 5.11)	1.34[b]
CHP4 (low fish density)					
Collector–gatherers	0.78	6.47 (4.63, 8.30)	0.45 (–0.28, 1.18)	7.69 (5.43, 9.30)	1.49[a]
Predators	0.83	18.67 (9.72, 27.62)	5.11 (0.37, 9.86)	9.24 (6.74, 11.15)	1.92[a,b]
Scrapers	0.32	100.10 (57.37, 142.83)	3.01 (0.00, 6.03)	67.08 (36.74, 85.48)	12.15[a,b]

Note: Analysis is presented for organization by functional feeding group (n = 48). Only groups with mean day 4 densities of three or more individuals are included.

[a]Significantly different from a random distribution (χ^2, $p < 0.05$).

[b]Degree of spatial aggregation increases with time (but is not significant).

[c]Distribution becomes significantly more contagious with time (linear regression, $n = 4$, $p < 0.05$).

Table 4. Regressions of log(mean + 1) and log(variance + 1) for each sampling day (both lakes pooled together) for data organized into orders.

Day	Slope[a]	SE	p	n
1	1.051[b]	0.194	0.001	9
2	1.499	0.210	0.0002	9
4	2.049	0.288	0.0002	9
8	1.959	0.174	<0.0001	9

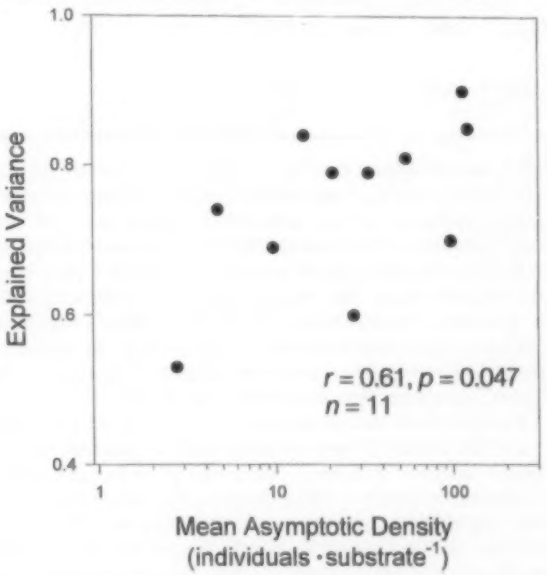
[a]Slopes differed, significant interaction term in ANCOVA, $F = 6.58$, $p = 0.0014$; only the slope of day 1 differed significantly from that of day 8.

[b]Not significantly different from 1 ($t = 0.26$, df = 9, $p > 0.50$); all other slopes were significantly different ($p < 0.05$).

Table 5. Mean (± SE) estimates of time to half saturation (B1), averaged over all taxa, for 3 levels of organization (taxonomic and feeding groups)

Level of organization	Mean	SE	n
Total invertebrates	2.83	0.20	2
Orders			
CPH3	7.02	3.67	4
CPH4	3.09	1.74	5
Functional feeding groups			
CPH3	4.66	2.17	4
CPH4	2.86	1.35	3

Fig. 4. Mean asymptotic density versus proportion of variance explained by the saturating function (R^2) for data organized by order (also including data for total invertebrate densities) for both lakes. Data were fitted using a parametric correlation with $\log_{10}(x + 1)$-transformed data to control heteroscedasticity.



able (26–72%), with an average overlap of 50.1 ± 5.09% (mean ± SE) (Table 6). Taxa that were generally found in the same proportion on artificial substrates as in diets (percent composition averaged over all lakes–dates on substrates versus diets) include Odonata (5.6% on substrates, 6.4% in diets), Trichoptera (1.6%, 1.2%), Amphipoda (39.8%, 60%), and Gastropoda (6.3%, 14.7%). Diptera were found more commonly on substrates than in diets. Of the other taxa sampled, Ephemeroptera and Turbellaria were rare or nonexistent in diets, but were more common on the substrates. Coleoptera and Hirudinea were rare both on the substrates and in diets. Hemiptera, a taxon that spends some time in the pelagic zone, is the only benthic macroinvertebrate taxon in which individuals were sometimes frequent in diets, but rare on artificial substrates.

Discussion

Benthic macroinvertebrates colonized artificial substrates set in vegetated littoral zones of several small lakes in south-central British Columbia. Measures of macroinvertebrate richness and abundance at several levels of taxonomic detail and functional feeding groups fit the theory of colonization provided by Michaelis–Menton kinetics. Times to half satu-

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Table 6. Percent by mass of macroinvertebrates captured on artificial substrates and in juvenile rainbow trout diets, with percent overlap calculated using Schoener's overlap index.

Lake	Year	Month	Sample	No. of samples	Proportion of macroinvertebrates per fish or tile					
					Ephemeroptera	Hemiptera	Odonata	Trichoptera	Coleoptera	Diptera
CPH1	1992	Sept.	Fish	38	0.0	6.5	15.8	0.0	3.2	1.2
			Tiles	12	9.7	0.1	9.0	3.7	0.0	54.2
CPH1	1992	Oct.	Fish	41	3.3	1.5	2.5	0.8	0.0	12.7
			Tiles	12	14.4	0.2	9.0	3.5	0.1	58.2
CPH2	1992	July	Fish	26	0.8	0.0	3.4	2.8	0.0	0.0
			Tiles	12	1.0	0.0	1.6	0.1	0.0	3.4
CPH2	1992	Sept.	Fish	28	0.0	0.0	0.5	1.5	0.0	0.0
			Tiles	12	6.4	0.0	7.1	0.9	0.0	12.0
CPH2	1992	Oct.	Fish	30	0.0	0.0	0.3	0.6	0.3	1.9
			Tiles	12	10.0	1.3	1.3	0.2	0.0	16.7
CPH4	1992	Sept.	Fish	16	0.0	0.0	0.5	0.3	0.3	0.0
			Tiles	12	11.3	0.2	14.3	0.9	0.0	12.1
BPH1	1993	Aug.	Fish	16	0.0	54.0	0.0	0.0	0.0	4.0
			Tiles	12	20.7	0.1	4.8	1.1	0.0	36.0
BPH2	1993	Aug.	Fish	17	0.0	0.0	1.2	1.2	0.0	27.6
			Tiles	12	3.2	0.0	6.2	5.0	0.0	56.6
CPH2	1993	Aug.	Fish	30	2.2	0.0	24.3	4.4	0.0	22.4
			Tiles	12	5.7	0.0	0.9	1.0	0.2	60.7
CPH4	1993	Aug.	Fish	14	1.3	0.0	15.7	0.0	0.3	0.0
			Tiles	12	10.8	0.0	2.1	0.0	0.0	2.1

ration varied among taxa, but a grand mean of 4 days was contained within all confidence intervals. Therefore, short-term colonization of our macrophyte mimic artificial substrates provides a reasonable estimate of relative abundance of the taxa sampled and of taxonomic richness within vegetated littoral zones. The mutual selectivity of the larger and more mobile macroinvertebrates by the artificial substrates and by a facultative benthivore suggests that the technique would be appropriate to assess the relative abundance of the macroinvertebrate taxa available to benthivorous fishes.

Knowledge of the colonization dynamics of artificial substrates is essential if they are to be used to quantitatively estimate benthic abundance (Rosenberg and Resh 1982; Boothroyd and Dickie 1989). In particular, it is necessary to have a good estimate of the time necessary for colonization to occur, whether judged by stabilization of species richness, stabilization of total invertebrate densities, or stabilization of densities within individual taxa (Mackay 1992). Previously, it was thought that implanted substrates should equilibrate to a point where the community on the substrates is exactly representative of the community in the system (Rosenberg and Resh 1982; Minshall and Petersen 1985). This particular equilibrium view may be unrealistic in that the macroinvertebrate community is likely made up of patches of organisms that differ markedly from each other in their local composition due to differences in microhabitat (Wetzel 1975). Although an accurate estimate of abundance can be made by taking many samples of such local populations, it is difficult to gauge at which point a substrate has reached equilibrium with the system. This is because this global equilibrium is simply a statistical average of patches that are themselves at various stages of colonization and have different local community composition. Therefore, there is no a priori reason to suggest that the community composition as a whole could be represented by individual patches that vary in their colonization state.

Issues of precision, accuracy, and duration of colonization can be addressed using our work, since we examined the temporal pattern of colonization. We propose that colonization has two components that determine the resulting community composition and abundance, a probabilistic component and a biological or behavioural component. In the early phases of colonization (<10 days), before the substrate has undergone significant modification (e.g., periphyton growth, accumulation of detritus), individuals will arrive on the substrate to assess its quality. Thus the change in numbers of individuals on the sampler will be a function of the balance between immigration and emigration rates. The large turnover rates during this period suggest that initial colonization is a random event (Boothroyd and Dickie 1991), and as a result, an equilibrium should eventually be reached where immigration equals emigration. Consequently, this should be a period in which a random and representative sample of macroinvertebrate abundance could be assessed.

The saturating colonization pattern that we have proposed for taxonomic richness and density is also prevalent among other studies (Townsend and Hildrew 1976; Peckarsky 1986; Boothroyd and Dickie 1989; Doeg et al. 1989*a*; Mathooko 1995). In these studies, time to half saturation was typically

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Proportion of macroinvertebrates per fish or tile					Total individuals counted	% overlap
Amphipoda	Hirudinea	Mesogastropoda	Pelecypoda	Tricladida		
35.7	0.0	25.8	11.8	0.0	771	32.7
18.6	0.1	2.0	1.8	0.9	1128	
57.8	0.0	20.6	0.8	0.0	1369	33.2
8.2	0.2	5.4	0.1	0.8	1040	
30.7	0.0	62.3	0.0	0.0	91	43.8
74.2	0.5	10.7	5.0	3.6	2346	
91.6	5.2	0.0	1.1	0.0	72	60.1
57.5	0.1	12.0	2.3	1.7	776	
74.8	0.0	19.6	2.4	0.0	382	71.7
58.1	0.2	9.4	1.7	1.1	958	
98.4	0.0	0.4	0.0	0.0	302	47.8
46.6	0.0	10.4	0.7	3.5	453	
42.0	0.0	0.0	0.0	0.0	248	26.5
22.3	0.1	6.0	2.3	6.5	788	
51.6	1.5	7.6	9.4	0.0	456	58.4
17.2	0.0	7.2	4.1	0.4	1118	
38.5	0.0	8.0	0.1	0.0	89	54.8
27.9	0.0	0.3	1.6	1.9	1025	
79.1	0.0	2.5	1.2	0.0	105	72.0
67.4	0.7	0.0	14.8	2.1	669	

between 1 and 3 days, but can be as high as 7–16 days. Lake and Doeg (1985) proposed that the best model to fit short-term colonization data is to use a regression model with log-transformed abundance. Although this provides a good statistical fit, the estimated parameters of the model have no direct biological interpretation. By using the Michaelis–Menton saturation function, the parameters are biologically interpretable. In contrast, the saturating colonization model appears to fit poorly with longer term data sets performed on the order of weeks and months (e.g., Peckarsky 1986; Doeg et al. 1989*a*; Boothroyd and Dickie 1991). Some of the more evident problems with this include increasing effects of seasonality (Doeg et al. 1989*a*), increasing modification of the substrate with time such as periphyton growth, increasing density effects, and effects of life history events (Meier et al. 1979).

There are thus trade-offs involved in selecting the appropriate colonization time for studies using artificial substrates. Estimating the relative density of a single taxon can be accomplished by performing a small-scale colonization experiment as was done in this study. For estimation of the relative densities of several taxa, a common colonization time is required. This is problematic given the range of estimates of time to half saturation across taxa. As we are interested only in the probabilistic nature of colonization due to encounters, we need to minimize the colonization period so as to minimize the confounding effects of interactions among individuals and effects of substrate quality change. A further argument for reducing the colonization interval is our observation that individuals become more contagiously distributed with time, resulting in higher variances and therefore lower precision. On the other hand, longer colonization intervals should result in colonization by less mobile species and a reduction in the probability that counts on the artificial substrates will vary strictly due to chance. Given these factors, a compromise in time interval can be reached for relatively short times, a result consistent with periphyton colonization of artificial samplers in which the most accurate estimates of density were made with short colonization intervals (Cattaneo and Amireault 1992). In our experiments, mean estimates for time to half saturation averaged across all taxa (for each level of organization) ranged from 2.8 to 7.0 days with a grand mean of 4 days. Using a 4-day colonization period to estimate relative abundance of macroinvertebrate taxa represents a reasonable estimate of colonization time, as it allows all taxa to be well into the colonization process, avoiding stochastic variation of low initial densities while still avoiding interactions among individuals. If the objective is to estimate taxonomic diversity, refinement of the sampling interval is recommended. We found that in the lake with potentially higher invertebrate densities, cumulative richness stabilized rapidly, and mean number of taxa decreased after day 4. However, in CPH3, the processes were slower, and a sampling beyond 4 days would be required. Therefore, diversity studies should include assessing the temporal pattern of colonization as we did in this experiment.

Improved fit of the colonization model with increased density of individuals within a taxon has implications for the precision of the relative density estimates. By increasing

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sampler size, it is possible to increase the density of organisms that are captured (Morin 1985). The colonizable surface area can be increased by adding a higher density of plastic macrophytes on each tile and the aerial span of the sampler. Increase in surface area should directly increase the carrying capacity of the sampler, while increased span should increase encounter rates with the substrate, although Giller and Cambell (1989) argued that a larger sampler will have less edge per unit area across which migration can occur. Augmenting the size of the sampler also means that fewer replicates would need to be taken for a particular level of precision (Morin 1985).

An unresolved issue is the accuracy with which the colonizing macroinvertebrates reflect the macroinvertebrate community of lakes (Rosenberg and Resh 1982; Morin 1987; Boothroyd and Dickie 1989). We did not attempt to address this issue by contrasting macroinvertebrate communities captured by various sampling devices. Clearly, various devices differ in their selectivity. Eckman grabs sample invertebrates on and below the surface of soft sediments, and sweep nets sample invertebrates in the water column and those on the extremities of macrophytes. Direct harvesting of macrophytes to capture invertebrates may be preferable, but colonizable surface area is difficult to control and the process is extremely time consuming. The artificial samplers that we designed and employed provide a relatively rapid technique and capture the larger and more mobile taxa found within macrophyte beds in littoral zones of lakes. Our artificial substrates should give accurate estimates of the *relative* abundance of macroinvertebrates because the colonization period involves a probabilistic random movement of individuals within a period that is short enough that the effects of succession are minimized, as evidenced by the observation that all taxa, with the exception of Chironomidae, reached asymptotes in the short term. Note that density estimates based on colonizing invertebrates can only be considered relative, as these estimates are not translated into aerial or volumetric densities. In addition, we observed overlap in selectivity of macroinvertebrate percent composition between our artificial substrates and diet of a facultative benthivore and found that substrates sampled all the taxa that were eaten by rainbow trout. In aggregate, the results of Konkle et al. (1990) with regard to overlap in biomass between samplers and diets, combined with our results for mutual taxonomic selectivity, suggest that artificial substrates can be used to provide estimates of relative availability of the benthic invertebrate taxa that are selected by visually foraging benthivores.

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References

Allan, J.D. 1984. Hypothesis testing in ecological studies of aquatic insects. *In* The ecology of aquatic insects. *Edited by* V.H. Resh and D.M. Rosenberg. Praeger Scientific, New York. pp. 484–507.

Boothroyd, I.K.G., and Dickie, B.N. 1989. Macroinvertebrate colonization of perspex artificial substrates for use in biomonitoring studies. N.Z. J. Mar. Freshwater Res. **23**: 467–478.

Boothroyd, I.K.G., and Dickie, B.N. 1991. Macroinvertebrate drift and community colonization on perspex artificial substrates in the Ohinemuri River, New Zealand. N.Z. J. Mar. Freshwater Res. **25**: 167–176.

Cattaneo, A., and Amireault, M.C. 1992. How artificial are artificial substrata for periphyton? J. N. Am. Benthol. Soc. **11**: 244–256.

Doeg, T.J., Lake, P.S., and Marchant, R. 1989*a*. Colonization of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. Aust. J. Ecol. **14**: 207–220.

Doeg, T.J., Marchant, R., Douglas, M., and Lake, P.S. 1989*b*. Experimental colonization of sand, gravel and stones by macroinvertebrates in the Acheron River, southeastern Australia. Freshwater Biol. **22**: 57–64.

Downing, J.A. 1979. Aggregation, transformations, and the design of benthos sampling programs. J. Fish. Res. Board Can. **36**: 1454–1463.

Downing, J.A., and Cyr, H. 1985. Quantitative estimation of epiphytic invertebrate populations. Can. J. Fish. Aquat. Sci. **42**: 1570–1579.

Dudley, T.L. 1988. The roles of plant complexity and epiphyton in colonization of macrophytes by stream insects. Verh. Int. Ver. Limnol. **23**: 1153–1158.

Edelstein-Keshet, L. 1988. Mathematical models in biology. Random House of Canada, Toronto, Ont.

Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Sci. Publ. No. 25. 2nd edition. Freshwater Biological Association, Ambleside, England.

Francis, D.R., and Kane, T.C. 1995. Effects of substrate on colonization of experimental ponds by Chironomidae (Diptera). J. Freshwater Ecol. **10**: 57–63.

Giller, P.S., and Cambell, R.N.B. 1989. Colonization patterns of mayfly nymphs (Ephemeroptera) on implanted substrate trays of different size. Hydrobiologia, **178**: 59–71.

Konkle, B.R., Collins, N.C., and Baker, R.L. 1990. Use of artificial substrates to estimate prey resources available to a visually feeding benthivorous fish. Can. J. Fish. Aquat. Sci. **47**: 789–793.

Krebs, C.J. 1989. Ecological methodology. Harper Collins Publishers, New York.

Lake, P.S., and Doeg, T.J. 1985. Macroinvertebrate colonization of stones in two upland southern Australian streams. Hydrobiologia, **126**: 199–211.

Mackay, R.J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Can. J. Fish. Aquat. Sci. **49**: 617–628.

Mathooko, J.M. 1995. Colonization of artificial substrates by benthos in a second-order high altitude river in Kenya. Hydrobiologia, **308**: 229–234.

Meier, P.G., Penrose, D.L., and Polak, L. 1979. The rate of colonization by macro-invertebrates on artificial substrate samplers. Freshwater Biol. **9**: 381–392.

Merritt, R.W., and Cummins, K.W. (*Editors*). 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendell/Hunt Publishing Company, Dubuque, Iowa.

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Minshall, G.W., and Petersen, R.C., Jr. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. Arch. Hydrobiol. **104**: 49–76.

Morin, A. 1985. Variability of density estimates and the optimization of sampling programs for stream benthos. Can. J. Fish. Aquat. Sci. **42**: 1530–1534.

Morin, A. 1987. Unsuitability of introduced tiles for sampling blackfly larvae (Diptera: Simuliidae). Freshwater Biol. **17**: 143–150.

Oertli, B., and Lachavanne, J.-B. 1995. The effects of shoot age on colonization of an emergent macrophyte (*Typha latifolia*) by macroinvertebrates. Freshwater Biol. **34**: 421–431.

Peckarsky, B.L. 1986. Colonization of natural substrate by stream benthos. Can. J. Fish. Aquat. Sci. **43**: 700–709.

Post, J.R., Parkinson, E.A., and Johnston, N.T. 1999. Density-dependent processes in structured fish populations: assessment of interaction strengths in whole lake experiments. Ecol. Monogr. In press.

Rosenberg, D.M., and Resh, V.H. 1982. The use of artificial substrates in the study of freshwater benthic macroinvertebrates. *In* Artificial substrates. *Edited by* J. Cairns. Ann Arbor Science Publishers, Ann Arbor, Mich. pp. 175–235.

Suren, A.M. 1991. Assessment of artificial bryophytes for invertebrate sampling in two New Zealand alpine streams. N.Z. J. Mar. Freshwater Res. **25**: 101–112.

Townsend, C.R., and Hildrew, A.G. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. J. Anim. Ecol. **45**: 759–772.

Wetzel, R.G. 1975. Limnology. 2nd ed. Saunders College Publishing, Philadelphia, Pa.

Wilkinson, L. 1992. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Ill.

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Influence of settlement time and size on postsettlement growth in the American lobster (*Homarus americanus*)

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Abstract: We investigated the size and timing of settlement of postlarval (fourth instar) American lobster (*Homarus americanus*) and the size attained by the end of the first growing season. Mean size and duration of benthic instars (IV–XI) were obtained from a field growth experiment. Lobsters settling in early- and mid-season were larger at each instar and had different growth profiles than late-season settlers. In particular, the rate of growth at the fifth and sixth instar transition was greater for early- and mid-season settlers than for late-season settlers. Postlarvae settling early reached the ninth instar sooner than mid- or late-season settlers. Estimates of size and intermolt duration of each instar for early- and late-season postlarvae were applied to planktonic postlarval data (1988–1995) to estimate growth trajectories during the first year. For all years, postlarvae present early in the season were 30–50% larger (carapace length) and two or three instars further developed than late settlers by the end of the growing season. Estimates of size attained by the end of the 1994 growing season matched field-collected benthic size frequency data for this same year. Although initial carapace length at settlement was important, the timing of settlement was more influential on the size attained by the end of the first growing season.

Résumé : Nous avons étudié la taille et le moment de l'établissement sur le fond marin des homards (*Homarus americanus*) postlarvaires (quatrième stade) ainsi que la taille atteinte au terme de la première saison de croissance. La taille moyenne et la durée moyenne des stades benthiques (IV à XI) ont été déterminées au moyen d'une expérience de croissance sur le terrain. Les homards qui se sont établis sur le fond au début ou au milieu de la saison de croissance (qualifiés ci-dessous de précoces) étaient plus grands à chaque stade et affichaient des caractéristiques de croissance différentes de celles des homards s'étant établis plus tardivement (tardifs). En particulier, le taux de croissance durant la transition entre les stades V et VI était plus élevé chez les homards précoces que chez les homards tardifs. Les postlarves précoces sont parvenues au stade IX plus rapidement que celles qui s'étaient établies vers le milieu de la saison ou plus tardivement. On a appliqué les estimations de la taille et de la durée de l'intermue de chaque stade des postlarves précoces et tardives aux données sur les postlarves planctoniques (1988–1995) afin d'estimer l'évolution de la croissance au cours de la première année. Pour toutes les années, les postlarves précoces étaient, à la fin de la saison de croissance, 30 à 50% plus grandes (longueur de la carapace) que les postlarves tardives, et elles avaient connu deux ou trois stades de plus que ces dernières. Les estimations de la taille atteinte à la fin de la saison de croissance de 1994 se comparaient à la distribution de fréquence de la taille observée au cours de la même année chez des spécimens récoltés sur les fonds marins. Si la taille initiale de la carapace au moment de l'établissement sur les fonds marins jouait un rôle important, le moment de l'établissement influait davantage sur la taille atteinte à la fin de la saison de croissance.

[Traduit par la Rédaction]

Introduction

Organisms with complex life cycles have a life history characterized by a metamorphosis, an abrupt ontogenetic change in morphology, physiology, and behavior that usually involves passage through two or more ecologically distinct phases (Istock 1967; Werner 1988). In insects and amphibians, the importance of size and timing of the ontogenetic habitat transition has been well documented (Wilbur 1980; Werner and Gilliam 1984). Generally, in these systems, a greater size and earlier time of habitat transition confer a survival advantage. Although most crustaceans have complex life cycles, little attention has been given to the consequences of variation in size and timing of ontogenetic

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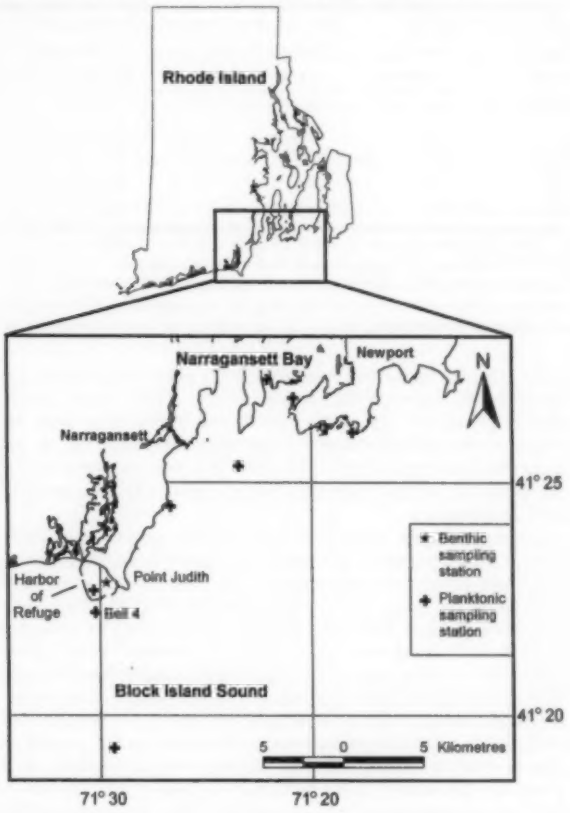
Fig. 1. Map of southern coastal Rhode Island showing planktonic postlarval and benthic sampling locations.



habitat shifts in this group of organisms. The early life history of the American lobster (*Homarus americanus*) provides an interesting opportunity to investigate the effects of the size and timing of the habitat transition in a crustacean. In this species, the molt between the third and fourth instars is a metamorphosis that results in a postlarva (fourth instar) that is anatomically, behaviorally, and physiologically distinct from the three previous larval instars (Charmantier et al. 1991). The postlarva remains in the plankton for most of the instar, making the transition to the benthic habitat toward the end of the postlarval instar. Soon after settlement to the benthos, the postlarva molts to the fifth instar, entering the "shelter restricted phase" of the lobster life cycle as defined by Lawton and Lavalli (1995). Thus the metamorphosis that begins at the postlarval molt is completed during the fifth instar (Charmantier et al. 1991).

There is little information on growth rates of newly settled lobsters in the field during the first growing season. While laboratory studies provide valuable information about factors that influence growth, they are probably not truly representative of growth attained in the field. Laboratory-reared larval lobsters, in general, differ from their wild counterparts. Previous work has shown that laboratory postlarvae are typically smaller, have weaker exoskeletons, are lighter in color, and have reduced growth rates compared with wild postlarvae (Lavalli 1991; Juinio and Cobb 1994; James-Pirri 1996; James-Pirri and Cobb 1997). Mean size and duration of larval and juvenile instars have been estimated from logarithmic equations and size frequency histograms (Templeman 1948; Wilder 1953; Mauchline 1977; Hudon 1987). Most of these estimates used pre- and post-molt relationships from adult lobsters to extrapolate the growth of smaller size classes. However, adult growth may not be representative of the growth of newly settled lobsters. There may also be regional differences in growth, and estimates from one locale may not be applicable to another.

The amount of growth attained prior to the habitat transition from the larval to the adult habitat may influence future juvenile growth and survival. It is not clear how much growth is accomplished during the first growing season or if it varies with time of settlement. It is likely that benthic individuals that attain a larger size by the end of the first growing season have a survival advantage. There is evidence that survival of the shelter restricted phase increases with size (Wahle and Steneck 1992). In southern New England, the newly settled cohort is easily distinguished from other year classes by size and timing of occurrence; however, it is not known what specific instars comprise that cohort (Incze and Wahle 1991; Wahle 1993). The growth parameters estimated in this study will aid in the accuracy of predicting the instar composition of the cohort newly recruited to the benthos. Identification of the composition of the first-year benthic cohort will contribute to our understanding of juvenile lobster growth and survival during the first year.

In this paper, we provide estimates of carapace length (CL) and intermolt duration for postlarval (fourth-instar) to 11th-instar lobsters reared in a field growth experiment. Growth estimates were applied to field data on planktonic postlarval size from 1988 to 1995 to obtain growth trajectories and to examine the hypothesis that variability in the size and timing of settlement influenced the size attained by the end of the first growing season. Size frequency distributions estimated from the growth trajectories were compared with actual field size frequency distributions of benthic lobsters. Growth factors and intermolt durations for instars IV–XI are compared with previous studies.

Methods and materials

Planktonic postlarvae collection

Planktonic postlarvae were sampled from two locations in Block Island Sound near Point Judith, Rhode Island (Harbor of Refuge and Bell 4), from 1988 to 1995 (Fig. 1). Postlarvae were collected from June to mid-August using paired neuston nets (500-μm mesh, mouth opening 1 × 0.5 m), equipped with flowmeters, towed from a small research vessel. Sampling for postlarvae started prior to the arrival of postlarvae in the neuston and ended 1 week after the last postlarvae were sampled for each year. This ensured that the start and end of the postlarval season (the period of time in days that postlarvae were present in the neuston) were recorded. All postlarvae were immediately removed from the sample and placed in jars of seawater held on ice. In the laboratory, carapace length for all postlarval lobsters was measured to the nearest 0.125 mm with a dissecting microscope and ocular micrometer. Molt cycle stage, an indicator of developmental age within a specific instar, was determined (Sasaki 1984). From molt cycle stage, we estimated the day of molting to the postlarval instar for each individual (Ta-

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ble 1). Time spent in the postlarval instar was determined using the molt cycle stage at the time of capture and the estimated percent duration of each molt cycle stage for the postlarval instar at a water temperature of 19°C calculated from Juinio (1991). The duration of molt cycle stages at 19°C was used because this temperature, of the temperatures that Juinio (1991) calculated intermolt duration for, best approximated the average surface temperature in the field in this region during the study period. For example, a planktonic postlarva caught in molt stage C has progressed through molt cycle stages A (0.5 day), B (1.0 day), and part of C (2.0 days); thus, it has been in the postlarval instar for about 3–4 days. Therefore, 3.5 was subtracted from the date of capture to obtain an estimate of the day of molt to the postlarval instar. Our estimates of molt cycle stage durations may be biased, since they rely on the laboratory data and assume an exposure to a constant temperature regime; however, at the present time, they are the only estimates available. Postlarvae collected in each year were designated as early or late settlers using the following criteria: the postlarval season was divided into quarters and postlarvae present during the first quarter were designated as early settlers and those present during the last quarter were late settlers. Data from individuals present in the second and third quarters of the postlarval season were omitted from the planktonic postlarval analysis, as we wanted to focus on extremes (early and late) of the postlarval season.

Field growth experiment

Postlarvae for the field growth experiment were collected at approximately weekly intervals in 1995 from the above two sampling locations and six additional locations in coastal Rhode Island in order to increase sample sizes for the treatments (Fig. 1). Postlarvae for the three settlement treatments were collected during a 25-day period spanning from June 26 through July 20 (an initial batch of postlarvae collected on June 19 died). As previously described, this period was divided into quarters and the settlement treatments were designated as follows: individuals from the first quarter were designated as the early settlement treatment, individuals from the second and third quarters as the middle settlement treatment, and individuals from the last quarter as the late settlement treatment. The early-season settlement was collected on June 26 (n = 17), the mid-season settlement on July 5 and 14 (n = 22 and 24, respectively), and the late-season settlement on July 17 and 20 (n = 14 and 9, respectively). Postlarvae were held in the laboratory in individual plastic mesh containers (8 cm in length by 6 cm in diameter, mesh size 1 × 2 mm) until they molted to the fifth instar (about 7–10 days from capture, depending on molt cycle stage). While in the laboratory, postlarvae were maintained in flowing, ambient temperature seawater and fed adult frozen brine shrimp ad libitum. Date of molt and carapace length were recorded for the fifth instar. After molting to the fifth instar, the lobsters, still in their individual containers, were randomly distributed among three wire-mesh cages. Cages were anchored off a dock at the University of Rhode Island's Graduate School of Oceanography campus on Narragansett Bay and rested on the bottom in about 7 m of water. The cages were about 40 cm square and were surrounded by 1-mm fiberglass mesh to prevent the entry of small fish and crabs. All lobsters were measured and fed (crab, fish, or mussel) about three times per week. Water temperature was recorded daily. Molt date was recorded when an exoskeleton was present in the container. On occasion, molt date had to be estimated if the lobster molted (and ate its exoskeleton) on a day in between feedings, as indicated by an increase in carapace length from one feeding day to the next. During the period from September 5 to 18, molt dates were not recorded, but feeding continued in the fashion described above. The field growth experiment was started July 5 and was terminated November 7, 1995. Average growth factors and intermolt duration of the instar (days) were calculated for each instar in each treatment group. Growth factor was calculated as the percent increase in carapace length between successive instars. Thus, instar-specific growth parameters for early, middle, and late settlers were obtained. Only lobsters that remained intact (no claw loss at any instar) for the duration of the field growth experiment were used in the estimation of instar carapace length, growth factor, and intermolt duration.

Table 1. Standardization of date of the postlarval molt based on molt cycle stage.

Molt cycle stage	% of instar duration	No. of days from molting to the postlarval instar	Estimated no. of days spent in postlarval instar
A and B	16	1–2	1.5
C	12	3–4	3.5
D_0	23	5–7	6
D_1	16	8–9	8.5
D_2	33	10–13	11.5

Note: Duration of instar is about 13 days at a water temperature of 19°C. Percent of time spent in each molt stage is estimated for this water temperature (based on laboratory data from Juinio 1991). The estimated number of days spent in the postlarval instar was subtracted from the date of capture to obtain an estimated date for molting to the postlarval instar.

Carapace lengths of early- and late-season postlarvae in 1988–1995 were compared using a t-test, and carapace lengths of early-, mid-, and late-season postlarvae of the field growth experiment were compared using analysis of variance (ANOVA). If a significant difference was found, the ANOVA was followed by a Tukey's multiple comparison test ($p < 0.05$) to determine which of the means were significantly different. Carapace length data from the field growth experiments for instars IV–IX were analyzed by repeated measures multivariate profile analysis (SAS Institute Inc. 1985) to determine if there were differences in the pattern of growth between treatments. This analysis was informative, as it tested for differences in the pattern of responses (i.e., growth in terms of carapace length size) (von Ende 1993). A summary of the hypotheses tested by the profile analysis is shown in Table 2. Contrasts between adjacent time periods (instars) allowed the identification of specific instars where differences in carapace length and rate of growth arose. If the treatment (settler) effect was significant in the contrast, a least significant difference test was used to compare differences among treatments. In this analysis, data from the 10th and 11th instars could not be included due to small sample sizes.

Times to the fourth to ninth instar for early-, mid-, and late-season settlement treatments were analyzed by failure time analysis (LIFETEST procedure, SAS Institute 1985). This analysis accommodated censored data, allowing the use of data points for their partial information, data that would have been omitted in other analyses. If the failure time analysis (Wilcoxon test) was significant, Z statistics were calculated for each pairwise comparison to determine which treatments were different (Fox 1993).

Estimates of growth

Instar- and settler-specific growth parameters (growth factor and intermolt duration) obtained from the field growth experiment were used to estimate growth trajectories and final size at the end of the growing season for early- and late-season planktonic postlarvae from the 1988–1994 cohorts. The end of the growing season was designated as October 1, after Hughes and Matthiessen's (1962) suggestion that in New England waters the last molt of the season occurs sometime during October. Planktonic postlarval data were first standardized by estimating the molt date to the postlarval instar for each individual as described previously (Table 1). Postlarval size (carapace length) and day of molt (to the postlarval

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Table 2. Summary of hypotheses tested by the repeated measures multivariate profile analysis and failure time analysis for the field growth experiment.

Null hypothesis tested	Statistical test	Result
Carapace length (growth) does not change with instar number	Profile analysis: time (instar) effect	$p = 0.0001$, H_0 rejected
Carapace length (growth) does not change with settlement treatment	Profile analysis: treatment (settler) effect	$p = 0.0254$, H_0 rejected
Rate of growth among instars and treatments is not different	Profile analysis: time × treatment interaction	$p = 0.0071$, H_0 rejected
Rate of growth between adjacent instars with time or treatment is not different	Profile analysis: ANOVA on contrast variables (time and treatment) followed by least significant difference test	Time: all contrasts, $p = 0.0001$*, H_0 rejected; treatment: contrast V–VI, $p = 0.0002$*, H_0 rejected
Time to reach the ninth instar does not differ between the settlement treatments	Failure time analysis followed by Z statistic	$p = 0.0005$, H_0 rejected

*Bonferroni adjusted alpha, $p < 0.0083$.

Table 3. Mean carapace lengths (CL, mm ± SD) for early- and late-season postlarvae collected from Harbor of Refuge and Bell 4 from 1988 to 1994 and duration (days) of postlarval season.

Year	Postlarval season start date (duration)	Early-season CL	Late-season CL	Size comparison	p
1995	June 13 (35)	4.44±0.23 (n = 39)	4.29±0.20 (n = 74)	Early > late	0.00
1994	June 16 (47)	5.09±0.21 (n = 23)	4.51±0.21 (n = 89)	Early > late	0.00
1992	June 16 (45)	4.95±0.23 (n = 135)	5.08±0.29 (n = 93)	Late > early	0.00
1991	June 6 (58)	4.63±0.27 (n = 254)	4.61±0.20 (n = 141)	Early = late	0.58
1990	June18 (52)	4.95±0.34 (n = 265)	4.82±0.29 (n = 81)	Early > late	0.00
1989	June 9 (50)	4.91±0.33 (n = 80)	4.97±0.38 (n = 54)	Early = late	0.34
1988	June 29 (31)	4.99±0.34 (n = 35)	4.47±0.27 (n = 135)	Early > late	0.00

Note: Postlarval season is the period of time in days that postlarvae were present in the neuston. Early- and late-season postlarvae were defined as individuals that were sampled as postlarvae during the first and last quarter of the planktonic postlarval season, respectively. Significance for early and late planktonic postlarval size comparison is given (t-test, $p < 0.05$).

instar) were used as the starting point for growth trajectories in all years. The final size (carapace length) and percent instar composition of early- and late-season settlers on October 1 were determined for each year class (1988–1994).

Early benthic phase lobsters

Early benthic phase lobsters were collected weekly from July 1 until August 25 and then once every other week in September 1994 from an area of suitable cobble substrate inside the Harbor of Refuge, Point Judith, Rhode Island (Fig. 1). Benthic samples were collected in about 5 m of water using SCUBA and a benthic air lift suction sampler. On each sampling day, at least eight 0.5-m^2 quadrats were haphazardly placed on suitable substrate and sampled. Benthic samples were sorted immediately and all lobsters were measured using vernier calipers. In 1993, there was an extremely low abundance of planktonic postlarvae (Incze et al. 1997; M.J. James-Pirri, personal observation). The few postlarvae in the plankton translated into a poor settlement cohort for 1993, which was the worst benthic recruitment year in this area since the initiation of benthic censuses in 1990 (Incze et al. 1997). Due to the low abundance of the 1993 cohort, benthic samples largely represented the 1994 recruiting year class. Since the 1994 cohort was clearly identifiable by size, the observed benthic lobster size frequency data from the Harbor of Refuge for September 1994 could be compared with the predicted size frequency distribution generated from the settler-specific growth parameters from the field growth experiment (using planktonic postlarval data from this same location). The size frequency distributions were compared using a Kolmogorov–Smirnov two-sample test. Statistical analyses were performed using SAS version 6.08 (SAS Institute Inc. 1985), SPSS version 7.0 for Windows, Microsoft Excel, and Statview.

Results

Postlarvae and field growth experiment

Postlarvae generally first appear in the plankton off southern Rhode Island in mid-June and are present through late July to early August (Table 3) (J.S. Cobb, unpublished data; James-Pirri 1996). Postlarvae present early in the season were significantly larger than postlarvae present late in the season in four (1995, 1994, 1990, 1988) of the seven years (t-test, $p < 0.5$; Table 3). Postlarvae present late in the season were larger than early-season individuals in only one of the years (1992). The year 1993 was a very poor year for postlarvae (only 65 individuals collected over the season), and therefore, that year was not examined.

Average bottom-water temperature during the growth experiment was 18.7 ± 2.9°C (range 24.5–13.4 °C). Since the three settlement treatments were placed in the field growth cages about 1 week apart during the month of July, the average daily water temperature for each treatment was compared. Average daily water temperature experienced by the three treatments was not significantly different (ANOVA, $p = 0.91$). Mortality was negligible for the duration of the growth experiment, except on one occasion, August 23, when a total of 19 individuals randomly distributed among

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Table 4. Average carapace lengths (CL, mm ± SD) of juvenile lobster stages IV–XI from the 1995 field growth experiment.

Instar	Early-season CL	Mid-season CL	Late-season CL	Overall average CL
IV	4.47±0.17 (n = 17)	4.32±0.16 (n = 42)*	4.22±0.22 (n = 23)	4.36±0.20 (n = 82)
V	5.13±0.19 (n = 17)	5.03±0.19 (n = 46)	4.82±0.29 (n = 21)	5.00±0.20 (n = 84)
VI	6.29±0.25 (n = 17)	6.04±0.35 (n = 45)	5.62±0.41 (n = 16)	6.01±0.41 (n = 78)
VII	7.33±0.29 (n = 17)	6.96±0.50 (n = 42)	6.54±0.55 (n = 15)	6.95±0.53 (n = 74)
VIII	8.46±0.34 (n = 14)	8.10±0.58 (n = 31)	7.74±0.72 (n = 15)	8.09±0.62 (n = 60)
IX	9.77±0.47 (n = 10)	9.53±0.68 (n = 27)	9.14±0.88 (n = 15)	9.46±0.73 (n = 52)
X	11.41±0.54 (n = 9)	11.14±0.74 (n = 23)	10.72±1.13 (n = 13)	11.07±0.86 (n = 45)
XI	12.90±0.72 (n = 3)	12.44±0.48 (n = 4)	—	12.63±0.59 (n = 7)

Note: Early-season settling lobsters were collected during the first quarter of the planktonic postlarval season, mid-season lobsters during the second and third quarters of the season, and late-season lobsters during the last quarter of the season. Overall average carapace length is the mean of the three treatments.

*Not all postlarvae initially measured.

Table 5. Average growth factors (± SD), expressed as proportions, for juvenile lobster stages IV–XI from the 1995 field growth experiment.

Instar transition	Early-season growth factor	Mid-season growth factor	Late-season growth factor	Overall average growth factor
IV–V	0.15±0.02 (n = 17)	0.14±0.03 (n = 42)*	0.15±0.04 (n = 21)	0.15±0.03 (n = 80)
V–VI	0.23±0.03 (n = 17)	0.20±0.05 (n = 45)	0.16±0.03 (n = 15)	0.20±0.05 (n = 77)
VI–VII	0.17±0.02 (n = 17)	0.15±0.05 (n = 42)	0.16±0.03 (n = 15)	0.15±0.04 (n = 74)
VII–VIII	0.16±0.03 (n = 14)	0.16±0.03 (n = 31)	0.18±0.04 (n = 14)	0.17±0.04 (n = 59)
VIII–IX	0.16±0.03 (n = 10)	0.17±0.03 (n = 26)	0.18±0.02 (n = 15)	0.17±0.03 (n = 51)
IX–X	0.17±0.01 (n = 9)	0.16±0.04 (n = 23)	0.17±0.03 (n = 13)	0.16±0.03•(n = 45)
X–XI	0.15±0.01 (n = 3)	0.16±0.01 (n = 4)	—	0.15±0.01 (n = 7)

Note: Early-season settling lobsters were collected during the first quarter of the planktonic postlarval season, mid-season lobsters during the second and third quarters of the season, and late-season lobsters during the last quarter of the season. The overall average growth factor is the mean of the three treatments.

*Not all postlarvae initially measured.

Table 6. Average instar duration (days ± SD) of juvenile lobster instars IV–X from the 1995 field growth experiment.

Instar	Early-season duration	Mid-season duration	Late-season duration	Overall average duration
IV	11.0±0.0 (n = 17)	10.1±2.5 (n = 42)	12.8±2.0 (n = 21)	11.0±2.4 (n = 80)
V	16.4±1.6 (n = 17)	15.3±2.6 (n = 38)	16.0±2.3 (n = 12)	15.7±2.5 (n = 67)
VI	14.7±2.1 (n = 15)	14.2±2.6 (n = 36)	15.3±2.3 (n = 12)	14.5±2.4 (n = 63)
VII	15.7±3.5 (n = 12)	17.0±3.6 (n = 21)	20.3±2.46 (n = 14)*	16.5±3.5 (n = 33)
VIII	16.8±1.1 (n = 6)	22.9±2.3 (n = 5)	20.3±2.46 (n = 14)*	19.0±4.0 (n = 11)
IX	27.8±5.8 (n = 5)	27.2±2.9 (n = 15)	23.8±3.0 (n = 13)	25.8±3.8 (n = 33)
X	29.0±4.0 (n = 3)	25.3±4.2 (n = 3)	—	27.2±4.2 (n = 6)

Note: Early-season settling lobsters were collected during the first quarter of the planktonic postlarval season, mid-season lobsters during the second and third quarters of the season, and late-season lobsters during the last quarter of the season. Overall average instar duration is the mean of the three treatments.

*Intermolt durations for instars VII and VIII late-season treatment were not available (due to missing data for the eighth-instar molt during the first 2 weeks of September). Durations were estimated by taking the midpoint of the instar VII–IX duration. These estimates were not in included when calculating the overall average intermolt duration for these instars.

the three cages were found dead. The cause of the mortality is unknown but may have been due to anoxic conditions, evidence of which was apparent in the containers of the dead individuals (sulfide smell and blackening of the containers).

Eighty-six lobsters (early season, n = 17; mid-season, n = 46; late season, n = 23) from the field growth experiment were used in the growth analysis. Early- and mid-season postlarvae were larger (ANOVA followed by Tukey's multiple comparison test, $p < 0.05$) than late-season postlarvae at the start of the experiment. Carapace lengths for each instar are shown in Table 4. Average growth factors between successive instars (V–XI) are shown in Table 5 and average intermolt durations are shown in Table 6. Duration for the seventh and eighth instar late-season treatment had to be estimated, by taking the midpoint between the known molting dates of the sixth and eighth instars, because of a 2-week period in September when molt dates were not recorded.

Carapace lengths between successive instars increased with instar number (MANOVA repeated measures profile analysis, p = 0.0001, all contrasts between adjacent instars,

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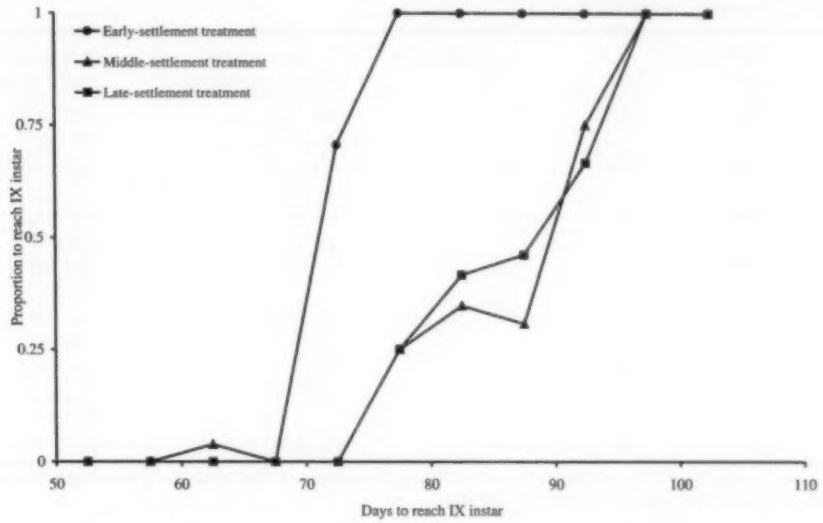
Fig. 2. Results of the failure time analysis: proportion of early-, mid-, and late-season treatments to reach the ninth instar in the field growth experiment.



$p = 0.0001$; Table 2), and growth of a given instar depended on the time of settlement ($p = 0.0254$; Table 2). The growth response profiles between the three treatments with time were also different ($p = 0.0071$; Table 2). Based on this, we conclude that the pattern of growth between the early-, mid-, and late-season settling treatments was significantly different. The only difference in the rate of growth between adjacent instars due to the settlement treatments was between the fifth and sixth instars ($F = 10.72$, df = 2, $p = 0.0002$, Bonferroni adjusted alpha, $p = 0.0083$; Sokal and Rohlf 1995). The growth increment for the instar V to VI transition was larger for early- and mid-season settlers than it was for late-season settlers (least significant difference test, $p < 0.05$). This was the only transition where a difference in the amount of growth between adjacent instars with treatment was observed.

Time to the ninth instar differed among treatments (SAS LIFETEST, Wilcoxon test, $p = 0.0005$; Fig. 2). The early-season lobsters reached the ninth instar at a significantly faster rate than mid- or late-season individuals (Z statistic, $p < 0.05$). Early-season lobsters reached the ninth instar in about 75 days whereas the mid- and late-season lobsters took up to 95 days. This was primarily due to the shorter duration of the seventh and eighth instars in early-season treatment (Table 6).

Estimates of growth

Planktonic postlarval size and back-calculated molt date to the fourth instar for early- and late-season individuals were used as starting points to estimate growth during a lobster's first growing season. Estimates of final size, percent size difference, and percent instar composition for early- and late-season lobsters on October 1 for the years 1988–1995 are shown in Table 7. The average growth trajectory for early- and late-season individuals over all years is shown in Fig. 3. Based on these estimates, the average size attained by the end of the first season's growth for juvenile lobsters would range from 8.0 to 12.5 mm CL, depending on the timing of settlement. By the end of the growing season, early-season lobsters were 30–52% larger than late-season lobsters. The instar composition of early- and late-season groups by the end of the growing season was very different. Early-season lobsters had reached instar IX or X whereas the late-season lobsters were in instars VIII and VII. A few late-season lobsters may be able to reach instar X, but this would only occur rarely (one out of seven years) and comprises a small percentage of the year class (3.7%) (Table 7).

To determine if seasonal timing of settlement or initial carapace length contributed more to overall differences in size by the end of the growing season, average growth was estimated holding each variable constant. When the time of settlement was held constant, the difference between early- and late-season lobsters at the end of the growing season was 7% (ninth instar 10.6 mm CL and ninth instar 9.9 mm CL, respectively). When the postlarval size was held constant, there was a 36% difference in carapace length (10th instar 11.8 mm CL and eighth instar 8.7 mm CL, respectively). The combination of variable size and timing of settlement created, on average, a 41% difference in size between early- and late-season lobsters by October 1 (10th instar 12.1 mm CL and eighth instar 8.6 mm CL, respectively). The estimated growth trajectories indicate that timing of settlement was more important in contributing to size differences at the end of the growing season than initial postlarval size differences.

Early benthic phase lobsters

The weekly size distribution of juvenile lobsters less than 20 mm CL sampled during 1994 is shown in Fig. 4. Since settlement was very poor in 1993, the 1994 cohort was clearly identifiable by size in the benthic samples. Size frequency data for September 1994 were compared with the predicted size frequency distribution generated from the growth parameters obtained from the field experiment. A

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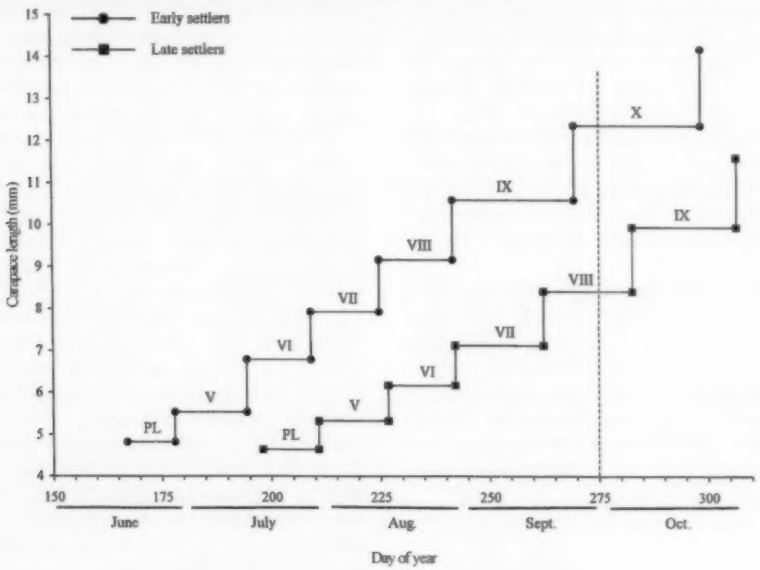
Table 7. Comparison of estimated carapace lengths (CL, mm), percent difference in size, and estimated percent instar composition of early- and late-season settling lobsters by the end of the growing season, designated as October 1, from 1988 to 1995.

Year	Estimated CL		% difference in CL	% early-season instar composition	% late-season settler composition
	Early	Late			
1995	10.92	8.33	31.0	IX: 28.2 X: 71.8	VIII: 60.8 IX: 39.2
1994	12.46	8.18	52.4	IX: 30.4 X: 69.6	VIII: 100.0
1992	10.98	8.14	35.0	IX: 93.3 X: 6.7	VII: 75.3 VIII: 24.7
1991	11.85	8.37	41.6	X: 100	VIII: 99.3 IX: 0.7
1990	11.67	8.67	34.3	IX: 56.6 X: 43.4	VII: 4.9 VIII: 95.1
1989	12.56	9.28	35.3	IX: 1.2 X: 98.8	VIII: 85.2 IX: 11.1 X: 3.7
1988	10.96	8.09	35.4	IX: 100	VIII: 100

Note: Estimates were obtained by applying instar and early- and late-season specific growth parameters (growth factors and instar duration) to planktonic postlarval data from each year.

Fig. 3. Growth trajectories for early- and late-season settling lobsters. Growth parameters for early- and late-season settlers were derived from the field growth experiment. Starting carapace lengths were averages for early- and late-season postlarvae (4.83 and 4.65 mm CL, respectively) from 1988 to 1995. Horizontal lines represent the length of the instar period and are centered on the average estimated carapace length for that instar. Vertical lines indicate the average increment between successive instars. The vertical broken line indicates the end of the growing season arbitrarily designated as October 1.



Kolmogorov–Smirnov two-sample test showed no significant difference between the predicted and actual size frequency distribution ($p = 0.20$), indicating that the growth estimates and predicted trajectories for the 1994 settling cohort were in agreement with the actual size distribution of lobsters sampled in September in the Harbor of Refuge. Additionally, the accuracy of the growth parameters was checked by back-calculating the size of the few larger lobsters sampled early in the season. In early July (July 3 and 10) and mid-August (August 6 and 15), nine lobsters in the 11- to 20-mm CL range were sampled (Fig. 4). Since postlarvae were not present in the plankton until June 16, 1994, it is unlikely that these individuals were from the 1994 settling year class. A conservative estimate of time to reach this size range is about 100 days (based on the growth parameters from the field growth experiment). Since these individuals were present 21 and 60 days, respectively, after the first appearance of planktonic postlarvae, they could not be from

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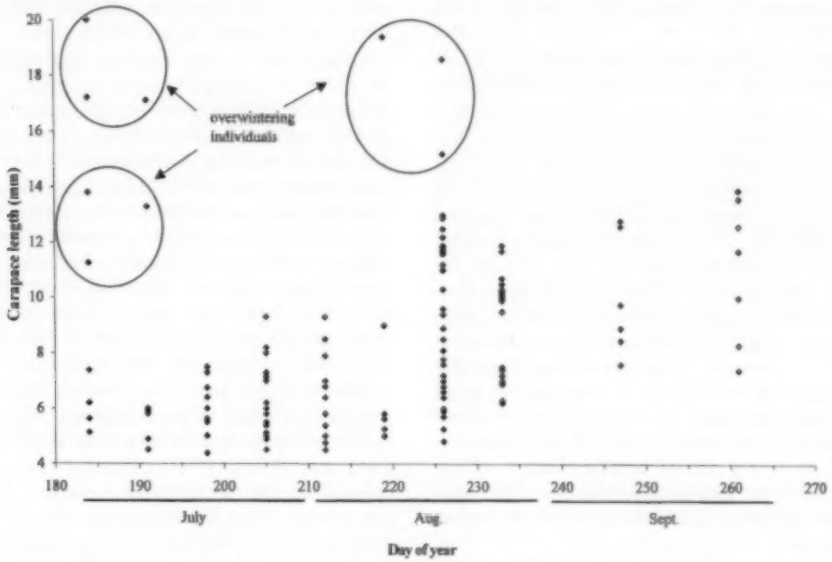
Fig. 4. Carapace lengths of benthic lobsters sampled on 10 dates during the summer of 1994. Overwintering lobsters from the previous year's cohort (1993) are circled.



the 1994 recruiting year class. Most likely they were individuals that settled late in 1993 and overwintered. Back-calculating the size (by two molts) of the three larger lobsters sampled in August (growth factor 15%, molt duration 26 days), they were estimated to be 14 mm CL in early July. This was similar in size to the six larger lobsters sampled in early July. The overwintering size of the lobsters sampled on July 3 and 10 (11–17 mm CL) can also be estimated. Assuming that these individuals had molted once in the spring prior to capture (since the first molt during a lobster's second year probably occurs sometime in May or June in New England waters; Hughes and Matthiessen 1962), we were able to estimate their overwintering size by back-calculating their size at the end of the previous season. Using an average growth factor of 15% (based on 11th-instar growth factor), the estimated overwintering size range for these lobsters is 9–14 mm CL, fitting within the predicted size range at the end of the growing season.

Discussion

Postlarvae present early in the season have a growth advantage over those present later in the season. Trajectories estimated from the growth parameters obtained from the field experiment indicate that juvenile lobsters will be 8–12.5 mm by the end of their first growing season, with early-season individuals being larger than lobsters that settled late in the season. Early-season postlarvae were larger than those present later in the season in four of the seven years. Hudon and Fradette (1988) similarly noted that early-season postlarvae were larger than those sampled later in the season.

Larger, early-hatching larvae may have better survival rates than later-hatching larvae. Lobster larvae hatched in the spring reached the fourth instar faster and survived better than those hatched in the late summer (Aiken et al. 1981, 1982). In culture, the first larvae to reach the fourth instar were also the largest (Eagles et al. 1986). Additionally, it has been suggested that survival is higher for early-hatching wild American lobster larvae exposed to rapidly increasing surface temperatures (Hudon and Fradette 1988).

Although carapace length at settlement affected the size attained during the first growing season, the timing of settlement was more influential. Individuals in the early-season treatment were larger and two or three instars more advanced than late-season individuals by October 1. The early-season treatment reached the ninth instar at a faster rate than mid- or late-season treatments. The most noticeable difference between early- and late-season settlement treatments was the average growth factor for fifth to sixth instar transition. Hudon (1987) also observed an increase in the growth factor at the fifth to sixth instar transition. She attributed this "growth spurt" to a higher abundance of food resources and sedentary habitats of newly settled lobsters. It is unlikely that a change to sedentary behavior played a role in the growth spurt we observed, since all treatments were reared equivalently. However, it is possible that in our experiment the lobsters may have fed on the plankton present in the water and that the early- and mid-season treatments were exposed to a different plankton prey field than the late-season treatment, causing the difference in the growth factors. Lavalli (1991) found that lobsters reared to the ninth instar showed higher survival and greater weight gain fed a diet of unfiltered seawater and brine shrimp versus filtered water and brine shrimp, indicating that juvenile lobsters can acquire additional nutritional substances from unfiltered seawater. Nutritional condition, as estimated by the ratio of RNA to DNA, of planktonic postlarvae decreases throughout the summer, presumably due to a changing prey field (Juinio and Cobb 1994). Juinio and Cobb (1994) found that planktonic postlarvae sampled off of southern coastal Rhode Island from 1988 to 1990 had a lower nutritional status in July than in June for two of those years (1989 and 1990). Addi-

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tional nutritional analyses of postlarvae sampled in 1991 and 1992 also showed significantly lower nutritional condition in July than in June (James-Pirri 1996; James-Pirri and Cobb 1997).

The first season's growth for newly settled lobsters is important, as small lobsters are likely to be quickly attacked by predators (Wahle and Steneck 1992). Postlarvae settling early in the season may reach a size-related predation refugium faster than the later-settling individuals. As body size increases, there is a geometrically declining risk of predation and increasing survival (Wahle 1992; Wahle and Steneck 1992). Wahle and Steneck (1992) observed that the number of predator attacks on tethered lobsters was greater for smaller (5–7 mm) than for larger lobsters (8–25 mm). Evidence from these studies suggest that the larger, early-season lobsters would have a higher probability of survival compared with smaller, late-season settlers. Hudon and Fradette (1988) similarly suggested differential survival for newly recruited benthic lobsters depending on whether postlarval settlement occurred early or late in the season. Large variations in growth rates of the newly settled benthic lobsters resulting in differential survival among individuals of the same year class may have important implications when the cohort recruits to the fishery.

Lobsters also may be subject to density-dependent mortality (Fogarty and Idoine 1986; Breen 1994). Postlarvae that settle early may have an advantage over later-settling postlarvae because densities are higher later in the season. However, there may be costs to settling early. Early settlers may experience lower water temperatures resulting in slower growth and a longer duration at a vulnerable size. There is some indication of initial slower growth for early-season settlers from this study. Duration of the fourth, fifth, and sixth instars was slightly longer for the early-season treatment. However, this difference was overcome within two molts when the early-season settlers reached the eighth instar sooner than the other treatments. It is unknown what contributed to the differences in the intermolt durations for these instars, but it may be related to a combination of temperature and changing planktonic prey field available to the lobsters. Other factors may also contribute to differential survival between early- and late-season settlers, such as seasonal differences in benthic predators or prey abundance; these areas merit further research.

The intermolt durations observed in this study were similar to those calculated by others (Wilder 1953, using Templeman's 1948 data; Mauchline 1977; Hudon 1987), yet the carapace lengths and growth factors observed in this study differ. In general the carapace lengths and growth factor estimates derived from these studies were larger than those reported here. Differences between this study and Templeman (1948), Wilder (1953), Mauchline (1977), and Hudon (1987) may be attributable to the use of a wide range of carapace lengths to generate growth equations used by these authors. These equations may not adequately represent growth of the smaller instars. Differences in instar sizes between this study and others may also be due to rearing the lobsters in captivity, and it is possible that the containers used in this study may have resulted in smaller growth increments. Container floor area can influence lobster size (Aiken and Waddy 1995); however, floor area may not have been a factor in this study. Since the mesh containers were neutrally buoyant and floated lengthwise, the lobsters were able to walk on the mesh, spinning the container. Thus the floor area available to the lobsters was essentially infinite.

Differences in sizes between equivalent instars may also be due to regional differences in temperature regimes or differences in larval origin.Thermal regime influences the onset of hatching, embryological and larval developmental rates, and planktonic food availability, which in turn affect growth rates (Aiken et al. 1982; Aiken and Waddy 1986). Southern New England may receive input from offshore stocks (Katz et al. 1994) that may have different growth parameters than inshore stocks. Additionally, southern New England itself may be quite different from other regions in terms of physical oceanographic and biological attributes that may result in physiological differences in growth rates for larval and juvenile lobsters (Aiken and Waddy 1986).

The estimated growth trajectories were in agreement with previous estimates of size attained by the end of the growing season (Hughes and Matthiessen 1962; Incze et al. 1997). Cobb and Wahle (1994) estimated instar duration based on thermal regime for different regions of the range of American lobster. They calculated that lobsters in southern New England, settling during peak abundance (late June), would be in the eighth instar by October 1. This is in agreement with the growth trajectories estimated in this study; early-season settling lobsters would be in the 10th instar and late-season settlers would be in the eighth instar. Hudon (1987) observed benthic lobsters less than 9 mm CL in May before the summer molting period in the Gulf of St. Lawrence. She suggested that these individuals had settled late the previous fall and therefore had undergone little growth through the winter months. These observations are also in agreement with the growth estimates observed in this study, which showed that individuals that settle late in the season would be about 9–11 mm CL the next spring, if sampled before undergoing the spring molt.

We observed that the timing of settlement resulted in size differences between early- and late-season individuals during the first year of growth. American lobster postlarvae that settled at the beginning of the season had as much as a 30- to 60-day growth advantage over those settling at the end of season, resulting in a possible two or three instar difference in development. Early-settling lobsters were larger at the end of the growing season and may have a competitive advantage over later-settling conspecifics. Although postlarval size at settlement had some influence on size at the end of the growing season, timing of settlement appeared to be more influential. Variation in size over the postlarval period may or may not occur; however there will always be variation in timing of settlement due to the extended period of time over which lobsters release their eggs (several weeks). An extended hatching period leads to a greater variability in settlement dates and thus a greater potential difference in instars between early- and late-season settling individuals.

The results of this study have given estimates of growth during the first few months of benthic life for the American lobster. We have shown that the postlarva, the transitional phase between the larval and the adult environment, is characterized by variable size and timing of settlement and that this variation results in differences in size at the end of the

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first growing season. Such size differences at the end of the growing season may affect survival during the winter and following spring.

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References

Aiken, D.E., and Waddy, S.L. 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. Can. J. Fish. Aquat. Sci. **43**: 2258–2270.

Aiken, D.E., and Waddy, S.L. 1995. Aquaculture. *In* The biology of the lobster, *Homarus americanus*. *Edited by* J.R. Factor. Academic Press, New York. pp. 153–175.

Aiken, D.E., Martin, D.J., Meisner, J.D, and. Sochasky, J.B. 1981. Influence of photoperiod on survival and growth of larval American lobsters (*Homarus americanus*). J. World Maricult. Soc. **12**: 225–230.

Aiken, D.E., Rowe, W.J., Martin-Robichaud, D.J., and Waddy, S.L. 1982. Seasonal differences in the effect of photoperiod on survival and development of larval American lobsters (*Homarus americanus*). J. World Maricult. Soc. **13**: 287–293.

Breen, P.A. 1994. Population dynamics and stock assessment of lobsters: a review. Crustaceana, **67**: 239–255.

Charmantier, G., Charmantier-Daures, M., and Aiken, D.E. 1991. Metamorphosis in the lobster, *Homarus* (Decapoda): a review. J. Crustacean Biol. **11**: 481–495.

Cobb, J.S., and Wahle, R.A. 1994. Early life history and recruitment processes of clawed lobsters. Crustaceana, **67**: 1–25.

Eagles, M.D., Aiken, D.E., and Waddy, S.L. 1986. Influence of light and food on larval American lobsters (*Homarus americanus*). Can. J. Fish. Aquat. Sci. **43**: 2303–2310.

Fogarty, M.J., and. Idoine, J.S. 1986. Recruitment dynamics in an American lobster *Homarus americanus* population. Can. J. Fish. Aquat. Sci. **43**: 2368–2376.

Fox, G.A. 1993. Failure-time analysis: emergence, flowering, survivorship, and other waiting times. *In* Design and analysis of ecological experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Chapman and Hall, New York. pp. 253–289.

Hudon, C. 1987. Ecology and growth of postlarval and juvenile lobster,*Homarus americanus*, off Iles de la Madeleine, Quebec. Can. J. Fish. Aquat. Sci. **44**: 1855–1869.

Hudon, C., and Fradette, P. 1988. Planktonic growth of larval lobster *Homarus americanus* off Iles de la Madeleine, Quebec, Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **45**: 868–878.

Hughes, J.T., and Matthiessen, G.C. 1962. Observations on the biology of the American lobster, *Homarus americanus*. Limnol. Oceanogr. **7**: 414–421.

Incze, L.S., and Wahle, R.A. 1991. Recruitment from pelagic to early benthic phase in lobsters *Homarus americanus*. Mar. Ecol. Prog. Ser. **79**: 77–87.

Incze, L.S., Wahle, R.A., and Cobb, J.S. 1997. Quantitative relationships between postlarval supply and benthic recruitment in lobsters, *Homarus americanus*. Mar. Freshwater Res. **48**: 729–743.

Istock, C.A. 1967. The evolution of complex life cycle phenomena: an ecological perspective. Evolution, **21**: 592–605.

James-Pirri, M.J. 1996. Growth and behavior during the settlement period of the American lobster, *Homarus americanus*. Ph.D. thesis, University of Rhode Island, Kingston, R.I.

James-Pirri, M.J., and Cobb, J.S. 1997. Growth rates of planktonic and newly settled American lobsters, *Homarus americanus*. Mar. Ecol. Prog. Ser. **160**: 233–240.

Juinio, M.A.R. 1991. Feeding ecology of the postlarval lobster *Homarus americanus*. Ph.D. thesis, University of Rhode Island, Kingston, R.I.

Juinio, M.A.R., and Cobb, J.S. 1994. Estimation of recent growth of field-caught postlarval American lobsters, *Homarus americanus*, from RNA:DNA ratios. Can. J. Fish. Aquat. Sci. **51**: 286–294.

Katz, C.H., Cobb, J.S., and Spaulding, M. 1994. Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. Mar. Ecol. Prog. Ser. **103**: 265–273.

Lavalli, K.L. 1991. Survival and growth of early juvenile American lobsters *Homarus americanus* through their first season while fed diets of mesoplankton, microplankton and frozen brine shrimp. Fish. Bull. U.S. **89**: 61–68.

Lawton, P., and Lavalli, K.L. 1995. Postlarval, juvenile, adolescent, and adult ecology. *In* The biology of the lobster, *Homarus americanus*. *Edited by* J.R. Factor. Academic Press, New York. pp. 47–88.

Mauchline, J. 1977. Growth of shrimps, crabs and lobsters. J. Cons. Cons. Int. Explor. Mer, **37**: 162–169.

SAS Institute Inc. 1985. SAS user's guide: statistics version 6.08 edition. SAS Institute Inc., Cary, N.C.

Sasaki, G.C. 1984. Biochemical changes associated with embryonic and larval development in the American lobster *Homarus americanus* Milne Edwards. Ph.D. thesis, Massachusetts Institute of Technology, Woods Hole Oceanographic Institute, Woods Hole, Mass. WHOI-84-8.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry the principles and practice of statistics in biological research. 3rd ed. W.H. Freeman and Co., New York.

Templeman, W. 1948. Growth per moult in the American lobster. Bull. Nfld. Gov. Lab. **18**: 26–48.

von Ende, C.N. 1993. Repeated measures analysis: growth and other time-dependent measures. *In* Design and analysis of ecological experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Chapman and Hall, New York. pp. 113–137.

Wahle, R.A. 1992. Body-size dependent anti-predator mechanisms of the American lobster. Oikos, **65**: 52–60.

Wahle, R.A. 1993. Recruitment to American lobster populations along an estuarine gradient. Estuaries, **16**: 731–738.

Wahle, R.A., and Steneck, R.S. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. **157**: 91–114.

Werner, E.E. 1988. Size, scaling, and the evolution of complex life cycles. *In* Size structured populations. *Edited by* B. Ebenman and L. Persson. Springer-Verlag, Berlin and Heidelberg. pp. 60–81.

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Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. **15**: 393–425.

Wilbur, H.M. 1980. Complex life cycles. Annu. Rev. Ecol. Syst. **11**: 67–93.

Wilder, D.G. 1953. The growth rate of the American lobster *Homarus americanus*. J. Fish. Res. Board Can. **10**: 371–412.

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Protective effects of water Cl^- on physiological responses to waterborne silver in rainbow trout

James C. McGeer and Chris M. Wood

Abstract: The importance of water Cl^- concentration in mitigating the effects of sublethal waterborne $AgNO_3$ exposure on rainbow trout was studied to test the relationship between physiological response and concentration of ionic silver (Ag^+). Trout were exposed to a total silver concentration of 30 nmol·L^{-1} (as $AgNO_3$) at a range of different water Cl^- concentrations from 20 to 1500 µmol·L^{-1}. These levels were chosen by speciation modelling with MINEQL+ to progressively reduce the concentration of Ag^+ largely by replacement with dissolved $AgCl_{aq}$. Fish exposed to $AgNO_3$ experienced a loss of Na^+; increasing the water Cl^- concentration reduced these losses. In vitro measurements after 50 h of exposure showed that Na^+ losses were related to Ag^+-induced inhibition of gill Na^+/K^+ ATPase activity; increasing the concentration of Cl^- in the water protected against the inhibition of Na^+/K^+ ATPase activity. The disruption of Na^+ regulation in $AgNO_3$-exposed fish was accompanied by increased plasma cortisol and total ammonia concentrations, but blood pH, plasma P_{CO_2} and HCO_3^-, and hematocrit were, in general, unaltered. Gill silver content increased in all $AgNO_3$-exposed trout and was not correlated with the disruption of Na^+ balance. We conclude that physiological measurements in combination with aquatic geochemical equilibrium modelling are useful in developing models to predict the acute toxicity of waterborne silver.

Résumé : Nous avons étudié dans quelle mesure la concentration de Cl^- dans l'eau atténue les effets de l'exposition hydrique de la truite arc-en-ciel à l'$AgNO_3$ pour examiner la relation entre la réaction physiologique et la concentration d'ions argent (Ag^+). Les truites ont été exposées à une concentration totale d'argent de 30 nmol·L^{-1} (sous forme d'$AgNO_3$), à une série de concentrations de Cl^- dans l'eau allant de 20 à 1 500 µmol·L^{-1}. Ces concentrations ont été choisies par modélisation de la différenciation à l'aide du MINEQL+ de façon à réduire progressivement la concentration d'Ag^+ en le remplaçant en bonne partie par de l'$AgCl_{aq}$ dissous dans l'eau. Les poissons exposés à l'$AgNO_3$ ont connu une baisse de Na^+; l'augmentation de la concentration de Cl^- a réduit cette déperdition. Les mesures in vitro effectuées après 50 h d'exposition ont montré que les déperditions de Na^+ étaient reliées à l'inhibition, induite par l'Ag^+, de l'activité branchiale de la Na^+/K^+ ATPase; l'augmentation de la concentration de Cl^- dans l'eau protégeait contre l'inhibition de l'activité de cette enzyme. La perturbation de la régulation du Na^+ chez les poissons exposés à l'$AgNO_3$ s'accompagnait d'une hausse des concentrations de cortisol plasmatique et d'ammoniac total, mais le pH sanguin, la P_{CO_2} et le HCO_3^- dans le plasma, de même que l'hématocrite, étaient globalement inchangés. La teneur en argent des branchies a augmenté chez tous les poissons exposés à l'$AgNO_3$, et n'était pas corrélée à la perturbation de l'équilibre du Na^+. Nous concluons que les mesures physiologiques, combinées à la modélisation de l'équilibre géochimique hydrique, sont utiles pour élaborer des modèles permettant de prévoir la toxicité aiguë de l'argent présent dans l'eau.

[Traduit par la Rédaction]

Introduction

Recently, silver has become a metal of toxicological interest and regulatory focus in North America and Europe (Hogstrand and Wood 1998). The presence of silver in the aquatic environment can arise as the result of anthropogenic inputs from many sources, including domestic and industrial discharges (Purcell and Peters 1998). In the environment, most silver is complexed to sulfide, chloride, and (or) dissolved organic carbon (DOC), depending on the water chemistry, and ionic silver (Ag^+) is usually <40% (usually substantially less) of total silver (Hogstrand and Wood 1998). $AgNO_3$ can be highly toxic to rainbow trout in freshwater with reported LC_{50} values ranging from about 60 to 120 nmol·L^{-1} or 6.5 to 13 µg·L^{-1} (Davies et al. 1978; Nebeker et al. 1983; Hogstrand et al. 1996). Although silver can be toxic at low concentrations, its acute toxicity is strongly influenced by chemical constituents in the water; Ag^+ is highly toxic whereas complexes of Ag^+ with sulphate, thiosulphate, Cl^-, and DOC are much less toxic (reviewed in Hogstrand and Wood 1998).

The varying acute toxicity of silver resulting from the complexation of Ag^+ to waterborne ligands conforms with the hypothesis proposed by Pagenkopf (1983) that the free ion form of a metal and its interaction with the fish gill are primarily responsible for acute toxicity (reviewed by Campbell 1995). For example, in rainbow trout (*Oncorhynchus mykiss*), the toxicity of $AgNO_3$, which readily dissociates to

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Table 1. Measured water Cl^- and total Ag concentration as well as calculated Ag speciation in the water Cl^- treatments used in exposures of rainbow trout to nominal concentrations of 30 nmol·L^{-1} $AgNO_3$. Prediction of Ag speciation was from the MINEQL+ software package and measured water quality variables. Only Ag species in which concentrations were altered by Cl^- content and >1% of the total Ag content are shown.

	Measured conc.		MINEQL+ predicted conc.			
Nominal water Cl^- treatment	Water [Cl] (μmol·L^{-1})	Total [Ag] (nmol·L^{-1})	[Ag^+] (nmol·L^{-1})	[$AgCl_{aq}$] (nmol·L^{-1})	[$AgCl_2^-$] (nmol·L^{-1})	[AgDOC] (nmol·L^{-1})
20 (control)	13	0	0	0	0	0
20	14	27.8	24.1	0.7	0.0	2.9
120	115	28.1	20.0	5.1	0.0	2.9
300	292	28.1	15.1	9.8	0.3	2.9
500	538	28.0	11.1	13.2	0.7	2.9
1500	1440	28.3	5.4	17.4	2.7	2.8

form Ag^+, is more than 13 000 times that of $Ag(S_2O_3)_n^{-(2n-1)}$, a compound that does not readily dissociate (Hogstrand et al. 1996). Waterborne Cl^- reduces acute $AgNO_3$ toxicity (LeBlanc et al. 1984; Hogstrand et al. 1996; Galvez and Wood 1997) through the reduction of Ag^+ concentration in the water and its replacement largely by dissolved $AgCl_{aq}$. The protective effect of water Cl^- is dramatic: Galvez and Wood (1997) demonstrated that the 7-day LC_{50} for juvenile rainbow trout increased from 30 to 920 nmol·L^{-1} (3.2 to 99 μg·L^{-1}) total silver in waters with 50 and 2500 μmol·L^{-1} (2 and 89 mg·L^{-1}) Cl^-, respectively. The combined works of Galvez and Wood (1997) and Hogstrand et al. (1996) clearly demonstrated a strong correlation between Ag^+ and acute toxicity because, irrespective of total silver and water Cl^- concentration, the 7-day LC_{50} value, as calculated from the geochemical modelling program MINEQL+ (Schecher and McAvoy 1992), was consistently 28 to 32 nmol·L^{-1} (3.0 to 3.5 μg·L^{-1}) Ag^+.

The primary physiological disturbance, and the presumed mechanism of toxicity, arising from exposure to $AgNO_3$ is an inhibition of Na^+ and Cl^- uptake at the gill with consequent declines in plasma Na^+ and Cl^- concentrations (Wood et al. 1996; Webb and Wood 1998). In turn, this leads to a suite of secondary effects, including blood acidosis, a generalized stress response, increased plasma total ammonia concentration, fluid volume disturbance, and hemoconcentration, which if severe, will lead to death as the result of cardiovascular collapse (Wood et al. 1996; Webb and Wood 1998; reviewed by Hogstrand and Wood 1998). Morgan et al. (1997) showed that this disruption of ion uptake in rainbow trout was primarily due to an inhibition of gill Na^+/K^+ ATPase activity. Na^+/K^+ ATPase is considered to be the key enzyme powering active Na^+ and Cl^- transport in freshwater fish (Wood 1992; Perry 1997). A preliminary study has suggested that the inhibition is due to Ag^+ blocking the binding of Mg^{2+}, a cofactor required for ATP hydrolysis (Ferguson et al. 1997).

The objective of our work was to understand the physiological nature of the protective effect of waterborne Cl^- on the sublethal toxicity of silver to rainbow trout (Hogstrand et al. 1996; Galvez and Wood 1997). All trout were exposed to 30 nmol·L^{-1} (3.2 μg·L^{-1}) total silver (added as $AgNO_3$) and water Cl^- was manipulated to alter the concentrations of Ag^+ and $AgCl_{aq}$ (plus small amounts of $AgCl_2^-$) in different treatments. The relative proportions of the silver species in each treatment were predicted using the geochemical modelling software package MINEQL+ (Schecher and McAvoy 1992). A detailed physiological study was conducted with particular focus on Na^+ balance and gill Na^+/K^+ ATPase activity in light of present knowledge of the mechanism of toxicity (Wood et al. 1996; Morgan et al. 1997).

Material and methods

Fish

Rainbow trout (320 g, $n = 39$) were obtained from a local commercial trout farm (Humber Springs, Orangeville, Ont.) and reared for at least 1 month in dechlorinated Hamilton tap water (ionic concentration: Na^+, 0.6 mmol·L^{-1}; Ca^{2+}, 1.0 mmol·L^{-1}; Cl^-, 0.7 mmol·L^{-1}; pH 8.0; temperature 15°C) before transfer to, and 3 weeks (minimum) acclimation in, soft water (ionic concentration: Na^+, 0.04 mmol·L^{-1}; Ca^{2+}, 0.04 mmol·L^{-1}; Cl^-, 0.04 mmol·L^{-1}; DOC, 0.3 mg·L^{-1}; pH 7.0), which was made by mixing reverse osmosis (Anderson Water Systems, Dundas, Ont.) partially purified water with dechlorinated Hamilton tap water. Prior to experiments, fish were starved for 2 days, anaesthetised with a $NaHCO_3$-buffered solution of 100 mg·L^{-1} MS222 (tricaine methanesulphonate; Sigma), surgically fitted with chronic indwelling dorsal aorta catheters for repeated blood sampling (Soivio et al. 1975), and transferred to individual 3L black perspex boxes, each with flowing aerated soft water (0.15 L·min^{-1}). Recovery was for 2 days before experimental procedures began, and cannulae were flushed daily with heparinzed (10 U·mL^{-1}) Cortland salmonid saline (Wolf 1963).

Exposure protocol

Fish were exposed for 50 h to 30 nmol·L^{-1} (3.2 μg·L^{-1}) total Ag in combination with a range of Cl^- treatments via a flow-through system that included a head tank into which concentrated $AgNO_3$ and KCl solutions (for adjustment of water [Cl^-]) were metered and then mixed with reverse osmosis generated (Culligan Water Systems, Hamilton) soft water (ionic concentration: Na^+, 0.04 mmol·L^{-1}; Cl^-, 0.02 mmol·L^{-1}; Ca^{2+}, 0.04 mmol·L^{-1}; DOC, 0.3 mg·L^{-1}; pH 7.0) by vigorous aeration before distribution to fish boxes. Water Cl^- treatments were chosen to cover the range normally found in fresh water; nominal concentrations ranged from 20 to 1500 μmol·L^{-1} (0.7 to 53 mg·L^{-1}). The measured water Cl^- concentrations and predicted silver speciation of treatments are shown in Table 1. Along with the five treatment groups, a sixth group of trout was subjected to the sampling protocol but not exposed to $AgNO_3$ (controls).

Serial blood samples (600 μL) from the dorsal aorta were taken before treatment (pre-exposure) and after 1.5, 6, 24, and 48 h of exposure. Blood was centrifuged, plasma was saved, and red blood

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cells were reconstituted in Cortland saline and returned to the fish via the catheter. After each blood sample, water flow to boxes was suspended for a period of 1.5 to 2 h and the volume was set to 2.7 L. Water samples (15 mL) were collected at the beginning and end of the period of box closure for measurements of net total ammonia and Na^+ fluxes as well as to confirm total silver and Cl^- concentrations. The flux measurements were performed before exposure began (pre-exposure) and then at 1.5–3, 6–8, 24–26, and 48–50 h of exposure.

After the 50-h of exposure, a lethal dose of anaesthetic (250 mg·L^{-1} MS222) was added to the box and the fish were quickly euthanized. Gill samples were collected, rinsed briefly (10 s) in exposure water without silver, immediately freeze clamped in liquid N_2, and then stored at –70°C.

Sample analysis, calculation, and statistics

Whole-blood pH was measured with a glass capillary electrode thermostated to the experimental temperature and connected to an acid–base analyser (PHM 71, Radiometer). Hematocrit was measured after centrifugation (5000 × *g* for 5 min). Plasma total CO_2 content was measured using a Capnicon 5 (Cameron Instruments). Partial pressure of CO_2 (Pco_2) and HCO_3^- concentration in plasma were calculated using the measured blood pH and total CO_2 values together with the pK′ and solubility coefficients for trout plasma from Boutilier et al. (1984). Plasma total ammonia (T_{amm}) concentration was measured with a commercial kit (Sigma 171 UV), water T_{amm} was measured by the salicylate hypochlorite method (Verdouw et al. 1978), and plasma cortisol was measured via radioimmunoassay (Immunocorp).

Water and plasma Na^+ concentrations were determined by atomic absorption spectrophotometry (AA1275 Varian) and water Cl^- was determined by the mercuric thiocyanate method of Zall et al. (1956). Gill filament tissue was digested in 5 volumes of 1 N HNO_3 (Janes and Playle 1995) and the total Ag concentrations of digested tissue and water were measured by graphite furnace atomic absorption spectrophotometry (AA1275 and GTA-95, Varian) as described by Galvez and Wood (1997).

The increases in water T_{amm} concentration that occurred in fish boxes of known volume during intervals when water flow was stopped were used to calculate T_{amm} excretion rates (Wright and Wood 1985). Changes in water Na^+ concentration were used to calculate net flux (Morgan et al. 1997).

Gill filament samples were assayed for Na^+/K^+ ATPase activity using the methods of Holliday (1985), described in detail by Morgan et al. (1997). Na^+/K^+ ATPase activity was expressed as the concentration of inorganic phosphate liberated per unit time and adjusted for the protein content of the sample (μmol PO_4·mg $protein^{-1}·h^{-1}$), the latter was determined using the dye binding assay of Bradford (1976). All spectrophotometric assays were modified for use with 96-well microtitre plates and microplate reader (MRX, Dynex), except for inorganic phosphate measurements of gill sample homogenates, which were measured in a cuvette-style spectrophotometer (LKB).

Results of 2-day exposures of trout to $AgNO_3$ were compared over time for each treatment or among treatments at 48 h by ANOVA and, when appropriate, Duncans New Multiple Range test. In all cases, $\alpha \leq 0.05$ was the accepted level of significance and data are shown as the mean ± 1 SEM.

Results

Control fish exhibited net Na^+ fluxes that did not differ significantly from zero throughout the 50-h experimental period (Fig. 1A). Additionally, plasma ions, acid–base status, and T_{amm} as well as T_{amm} excretion rate and hematocrit were stable in control fish (Table 2). Cortisol declined slightly with time (Fig. 1B). Thus the experimental procedures had minimal influence on the parameters measured.

Exposure to 30 nmol·L^{-1} $AgNO_3$ resulted in a significant disruption in Na^+ balance in rainbow trout, the effects of which were reduced with increasing water Cl^- concentration. At the low Cl^- concentration of 20 μmol·L^{-1}, plasma Na^+ declined continuously and at 48 h differed significantly from pre-exposure measurements (Table 2). In general, the declines in plasma Na^+ concentration by 48 h were less as water Cl^- concentrations increased (Table 2). Changes in plasma Cl^- tended to parallel those in the plasma Na^+, but none of the Cl^- alterations was significant (Table 2). In conjunction with the loss of plasma Na^+, all fish exposed to silver (except those at the highest Cl^- level tested) showed a significant net loss of Na^+, particularly in the first day of exposure (Fig. 1A). In general, the net loss of Na^+ was reduced with increasing water Cl^- level, particularly at 48 h (Fig. 1A). Cortisol was significantly increased in most trout exposed to Ag^+ (Fig. 1B), and during the first day, fish with a significant loss of Na^+ also showed elevated cortisol levels (Figs. 1A and 1B).

Gill Na^+/K^+ATPase activity complemented the pattern of Na^+ loss from $AgNO_3$ exposed trout. In water of low Cl^- concentration, Na^+/K^+ATPase activity was severely inhibited (80%) relative to control values (Fig. 2A), but as Cl^- increased, this inhibition decreased (Fig. 2A). When expressed as a function of the Ag^+ concentration, as calculated by MINEQL+, the inhibition of Na^+/K^+ATPase was highly correlated with Ag^+ ($r^2 = 0.98$, $n = 5$; Fig. 2B).

In spite of the protective effect that increasing Cl^- had on Na^+ loss (Fig. 1, Table 2) and gill Na^+/K^+ ATPase activity (Fig. 2), the accumulation of silver in the gill did not vary. Branchial total Ag content was elevated relative to unexposed fish in all silver-exposed trout and there were no significant differences among Cl^- treatments (Fig. 3).

Exposure to waterborne $AgNO_3$ did not result in any consistent acid–base disturbances; but plasma T_{amm} accumulated in all exposed fish and this accumulation was similar among Cl^- treatments (Table 2). In spite of increased plasma T_{amm} content, there was no increase in T_{amm} excretion (Table 2).

Discussion

These experiments support previous reports that water Cl^- has a protective effect on $AgNO_3$ toxicity (Galvez and Wood 1997; Hogstrand et al. 1996) and suggest that at least part of the mitigation of toxicity is via a reduction of the inhibitory effect that silver has on gill Na^+/K^+ ATPase activity. As waterborne Ag^+ and Cl^- form complexes, free Ag^+ concentration is reduced, inhibition of branchial Na^+/K^+ ATPase is reduced, and the disruption of Na^+ balance in the fish is minimized. These results may provide a physiological explanation for the protective effect of water Cl^- on the acute toxicity of $AgNO_3$ (Galvez and Wood 1997; Hogstrand et al. 1996) and provide a model for studying the effects of water chemistry on sublethal silver exposure.

The concept that geochemical characteristics of the water influence the toxicity of waterborne heavy metals has been recognized previously (Babich and Stotzky 1983; Campbell and Stokes 1985; Newman and Jagoe 1994; Allen and Hansen 1996). However, the protective effect that water Cl^- ex-

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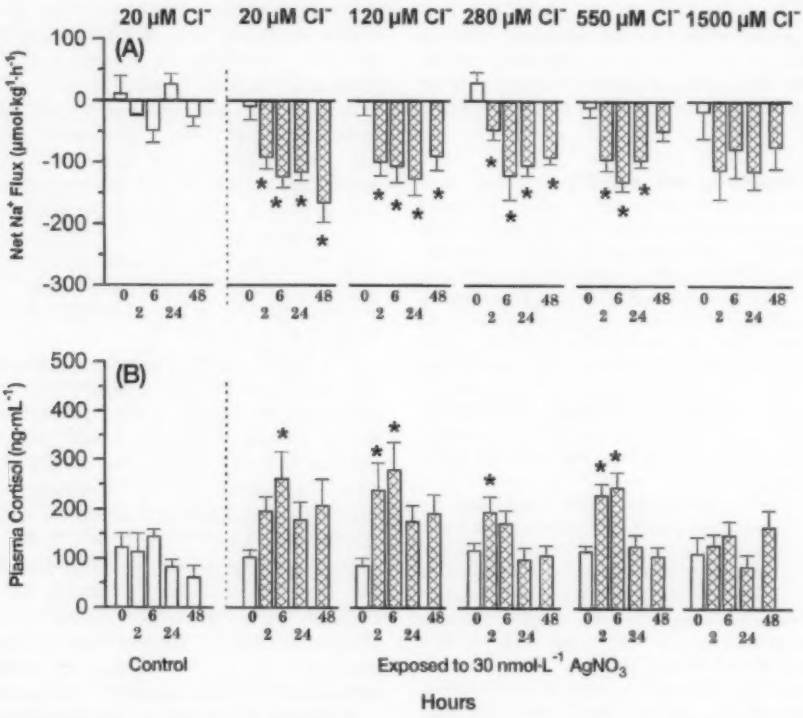
Fig. 1. (A) The net flux of Na^+ and (B) plasma cortisol concentration in groups of rainbow trout exposed to 30 nmol·L^{-1} total Ag (as $AgNO_3$, cross-hatched bars) over 50 h in water with different water Cl^- treatments ranging from 20 to 1500 μmol·L^{-1}. The net flux was measured over 1.5 to 2 h with positive bars indicating a net movement of Na^+ into fish and negative bars indicating a net loss of Na^+ from fish. Within each water Cl^- treatment, Na^+ flux and plasma cortisol were measured before exposure began (0 h) and at 2, 6, 24, and 48 h and in a group of trout similarly sampled but not exposed to $AgNO_3$ (control, open bars). Mean (± SEM) from at least six fish are shown, except for controls where n = 4. * indicates a significant difference from the pre-exposure measurement for that treatment.



erts on the acute toxicity of silver is not specifically recognized in the water quality guidelines–criteria of regulatory bodies such as Environment Canada or the United States Environmental Protection Agency (U.S. EPA). The latter agency does recognize a protective role for one water chemistry variable only, specifically water hardness (U.S. EPA 1980). However, Hogstrand et al. (1996), Galvez and Wood (1997), and Hogstrand and Wood (1998) argued that this protective role for hardness was based on a misinterpretation of original data. Galvez and Wood (1997) suggested that the most important protective agent in the original data set used to derive the U.S. EPA (1980) "hardness equation" for acute Ag toxicity was Cl^- and not hardness, although the latter did exert a relatively minor protective influence. While we did not measure acute toxicity directly, our study supports the conclusion that water Cl^- protects against the deleterious effects of waterborne Ag^+. DOC, a naturally occurring anionic ligand that strongly binds Ag^+ (Janes and Playle 1995), is another geochemical factor that might influence silver toxicity in a similar manner.

Our study also provides more evidence that complexed silver causes significantly less sublethal physiological effect than does Ag^+ and demonstrates that predictions of Ag^+ concentration derived from relatively easy-to-use computer packages correlate well with one of the suggested mechanism of toxicity (Morgan et al. 1997). The combination of a sensitive physiological measure, such as inhibition of gill Na^+/K^+ ATPase activity, with geochemical speciation modelling software packages, such as MINEQL+ (Schecher and McAvoy 1992), may provide a method for developing models that will predict the acute toxicity of silver on a site-specific basis. New approaches based on speciation modelling, such as the gill receptor loading model, have recently been endorsed as possible tools for predicting acute metal toxicity (Bergman and Dorward-King 1997).

The direct relationship between Ag^+, acute toxicity (Hogstrand et al. 1996; Galvez and Wood 1997), and in this study, sublethal Ag^+ and gill Na^+/K^+ ATPase activity indicates that responses of trout to waterborne silver conform to the gill surface interaction (Pagenkopf 1983) or free ion activity model (reviewed by Campbell 1995). This model is based on the assumptions that different chemical species of a metal have differing toxicities, that the species that are toxic bind to the gill, and that they then exert a biological effect that is exhibited, ultimately, as a toxic effect. Our work indicates that ionic Ag^+ acts on the gill at a specific site, the Na^+/K^+ ATPase enzyme system, in a dose-dependent manner resulting in disruption of Na^+ balance in the fish. The mechanism of sublethal toxicity may therefore be similar to that of Cu^{2+} (Pagenkopf et al. 1974; Laurén and McDonald 1987;

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Table 2. Blood and plasma variables from rainbow trout exposed to 30 nmol·L^{-1} total Ag (as $AgNO_3$) over 48 h in different water Cl^- treatments ranging from 20 to 1500 μmol·L^{-1}.

	Treatment		Time of exposure (h)				
	Total [Ag] (nmol·L^{-1})	Water [Cl^-] (μmol·L^{-1})	Pre-exposure	1	6	24	48
Blood pH	0	20	7.86±0.03	7.92±0.05	7.91±0.06	7.82±0.02	7.83±0.03
	30	20	7.88±0.02	7.89±0.02	7.86±0.03	7.90±0.01	7.88±0.04
	30	120	7.85±0.04	7.83±0.03	7.86±0.04	7.91±0.04	7.93±0.05
	30	300	7.84±0.04	7.82±0.03	7.87±0.03	7.87±0.03	7.89±0.04
	30	500	7.88±0.02	7.91±0.04	7.89±0.06	7.92±0.05	7.83±0.05
	30	1500	7.89±0.02	7.86±0.02	7.85±0.03	7.87±0.02	7.84±0.04
Plasma P_{CO_2} (torr)	0	20	2.8±0.2	2.1±0.2	2.4±0.4	3.1±0.5	2.6±0.2
	30	20	2.4±0.1	2.9±0.3	2.9±0.2	2.2±0.4	2.4±0.2
	30	120	2.5±0.1	2.5±0.1	2.2±0.2	2.2±0.1	1.8*±0.1
	30	300	2.5±0.3	3.0±0.2	2.9±0.3	2.9±0.2	2.1±0.2
	30	500	2.8±0.2	2.5±0.2	2.4±0.2	2.1±0.2	1.9±0.4
	30	1500	2.5±0.2	2.6±0.3	2.5±0.2	2.1±0.2	1.7±0.3
Plasma HCO_3^- (mmol·L^{-1})	0	20	7.5±1.2	6.5±1.0	7.2±1.2	7.3±1.2	6.4±0.2
	30	20	6.7±0.5	7.9±0.8	7.7±0.8	6.6±1.1	6.9±0.7
	30	120	6.6±0.6	6.4±0.6	5.8±0.6	6.7±0.4	5.6±0.6
	30	300	6.1±0.7	7.3±0.6	7.5±0.7	7.9±0.6	6.0±0.8
	30	500	7.6±0.6	7.7±0.9	7.0±1.0	6.5±0.8	4.6±0.9
	30	1500	7.1±0.8	6.9±0.8	6.4±0.7	5.6±0.3	4.1*±0.7
Plasma Na^+ (mmol·L^{-1})	0	20	142±2.7	142±5.0	138±4.8	136±3.8	138±4.3
	30	20	137±2.6	134±3.1	130±3.3	129±3.3	121*±3.1
	30	120	139±2.3	138±3.2	138±2.8	135±3.4	131±5.3
	30	300	138±2.7	137±3.7	137±3.4	133±2.8	134±5.2
	30	500	137±5.0	141±5.4	142±3.6	135±3.1	136±2.5
	30	1500	138±4.3	141±4.4	145±5.6	140±6.0	139±5.7
Plasma Cl^- (mmol·L^{-1})	0	20	119±3.9	119±3.5	124±4.5	120±4.8	119±4.8
	30	20	116±4.5	117±4.1	117±3.6	113±3.7	104±6.8
	30	120	121±3.0	122±4.3	121±3.7	118±4.5	113±6.6
	30	300	118±4.6	114±3.6	117±3.5	113±3.6	112±4.1
	30	500	120±3.5	121±3.4	121±3.0	120±3.2	119±4.1
	30	1500	117±3.7	120±4.9	116±5.9	115±6.0	112±6.9
Plasma T_{amm} (μmol·L^{-1})	0	20	78±30	60±24	78±28	41±31	29±18
	30	20	69±15	137*±14	152*±14	161*±22	185*±30
	30	120	41±6	62±13	116*±16	258*±33	181*±28
	30	300	68±8	106±14	154*±18	214*±28	190*±35
	30	500	51±14	108±24	174*±35	280*±49	268*±39
	30	1500	52±10	75±9	149*±5	199*±49	170*±39
T_{amm} excretion (μmol·kg^{-1}·h^{-1})	0	20	343±80	391±73	438±111	375±109	404±104
	30	20	334±27	316±26	339±28	372±43	456±59
	30	120	231±23	246±25	252±26	334±31	328±49
	30	300	258±63	319±57	345±64	394±72	364±53
	30	500	224±27	188±43	271±39	317±31	393±13
	30	1500	300±58	295±39	293±57	403±35	377±47
Hematocrit (%)	0	20	33±1.7	34±1.7	32±3.2	27±2.6	26±3.5
	30	20	31±1.4	29±1.4	30±1.3	32±1.7	30±2.2
	30	120	29±2.1	29±2.1	27±1.8	27±1.9	28±2.3
	30	300	30±2.8	30±1.9	28±1.9	26±2.2	27±2.6
	30	500	33±2.5	31±2.1	30±2.6	27±2.2	28±1.8
	30	1500	27±3.4	27±2.9	27±2.6	29±2.7	34±3.0

Note: Control fish were kept in 20 μmol·L^{-1} [Cl^-], in the absence of $AgNO_3$. Total ammonia excretion was measured over 1.5 to 2 h immediately after blood sampling. Within each treatment, samples were collected before exposure began (0 h) and at 1.5, 6, 24, and 48 h. Mean (± SEM) from at least six fish (except for controls where $n = 4$) are shown. * indicates a significant difference from the pre-exposure mean for that treatment.

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Fig. 2. Relative Na^+/K^+ ATPase activity of gill tissue from rainbow trout exposed to 30 nmol·L^{-1} total Ag (as $AgNO_3$) for 50 h expressed in relation to (A) water Cl^- treatments (cross-hatched bars) and (B) water ionic Ag^+ concentration (solid circles). Ionic Ag^+ concentration was calculated using MINEQL+ software and measured water quality values (Table 1). A group of unexposed fish similarly treated but not exposed to $AgNO_3$ is also shown (controls, open bar in A and open circle in B). Means (± SEM) from at least six fish (except for controls where $n = 4$) are shown. In panel A, * indicates a significant difference from controls ($P < 0.05$), whereas for silver-exposed fish, means tagged with the same letter are not significantly different. In panel B, a best-fit regression line is included (Na^+/K^+ ATPase activity = 2.57 − 0.097 ([Ag^+]), $r^2 = 0.98$, $n = 5$).

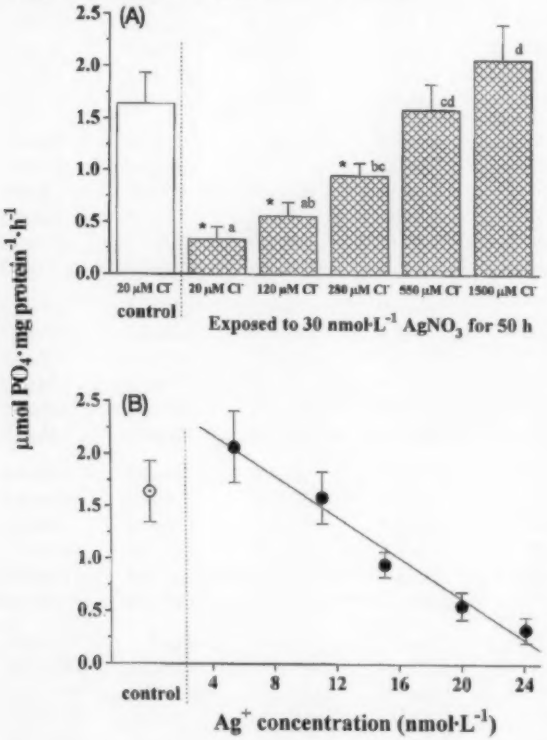
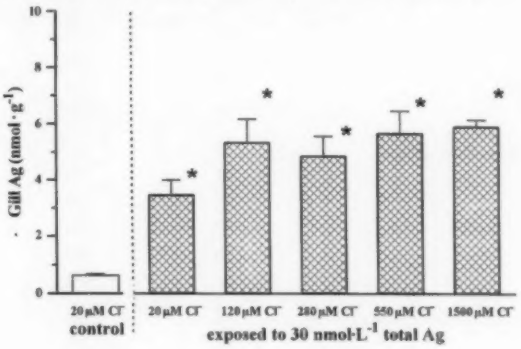


Fig. 3. Total Ag burden in gills of rainbow trout exposed to 30 nmol·L^{-1} total Ag (as $AgNO_3$, cross-hatched bars) over 50 h in water with Cl^- concentrations ranging from 20 to 1500 μmol·L^{-1}. Mean (+ SEM) from at least six fish are shown (except for controls where $n = 4$); * indicates a significant difference from controls. There were no significant differences in gill total Ag burden among silver-exposed fish ($P < 0.05$).



Allen and Hansen 1996; Li et al. 1996). This similarity between Ag^+ and Cu^{2+} occurs in spite of the fact that inorganic speciation in freshwater for copper is dominated by hydroxide and carbonate complexation (i.e., pH and alkalinity) whereas that for silver is influenced primarily by Cl^- complexation (Morel and Hering 1993).

Three physiological measures of Na^+ balance were used in these experiments, with activity of gill Na^+/K^+ ATPase being the most sensitive in illustrating the effect of Ag^+ (Fig. 2B). The protective effect of Cl^- on Na^+ balance, as measured by plasma Na^+ values and net flux of Na^+, was significant but less distinct compared with the protection of gill Na^+/K^+ ATPase activity. This may be because plasma Na^+ and net flux of Na^+ are secondary, or more general, measures of Na^+ balance. Plasma Na^+ levels will be influenced by water balance and movements of Na^+ from other internal compartments (e.g., Audet et al. 1988). Net Na^+ flux is the result of unidirectional Na^+ uptake as well as unidirectional Na^+ loss and, therefore, will be a less sensitive measure because Ag^+ exposure affects only unidirectional Na^+ uptake (Morgan et al. 1997; Webb and Wood 1998).

An important finding of the present study was that with increasing water Cl^- concentration, there was no relationship between water Ag^+ concentration and accumulation of silver on the gills. Furthermore, there was no relationship between the gill silver burden and one of the principal physiological effects of Ag^+, the inhibition of branchial Na^+/K^+ ATPase activity. All trout exposed to $AgNO_3$ experienced similar gill total Ag burdens after 50 h (Fig. 3). These results are similar to the data of Janes and Playle (1995), who showed that total Ag accumulation on the gills of rainbow trout after 3 h of exposure to 110 nmol·L^{-1} (12 μg·L^{-1}) $AgNO_3$ in soft water was not affected by water Cl^- concentrations up to 1500 μmol·L^{-1} (53 mg·L^{-1}). Janes and Playle (1995) interpreted this as a result of the higher conditional equilibrium binding constant for Ag^+–gill (log K value 10) compared with that for Ag^+–Cl^- (log K value of 5.3). However, Janes and Playle (1995) interpreted all gill accumulation, including that occurring at high Cl^- levels, as toxic Ag^+ binding. In contrast, the current study suggests that accumulation of Ag in the gill may occur as a result of both Ag^+–gill binding (toxic) and AgCl accumulation (relatively non-toxic). The latter apparently predominated at high water Cl^- levels. The mechanisms of accumulation of AgCl complexes in the gill are unknown but could occur as AgCl–gill binding and (or) as diffusion of neutral $AgCl^0$ into the gill epithelium. The possibility of mixed ligand–metal complexes (e.g., Cl–Ag–gill) was recognized as a potential complicating factor in the development of the free ion activity model (Newman and Jagoe 1994; Campbell 1995). Studies on the gill uptake characteristics of waterborne AgCl complexes (e.g., AgCl–gill conditional equilibrium binding constant or $AgCl^0$ diffusion coefficient) and a further exploration of the relationships between gill total Ag burdens resulting from different

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exposure chemistries and toxicity are required if a model to predict acute silver toxicity is to be successful.

The disruption of Na^+ balance in rainbow trout exposed to Ag^+ was accompanied by an increase in plasma cortisol and T_{amm} content but few other significant changes in the measured physiological variables (Table 2). The increase of plasma cortisol was only significant at 2 and (or) 6 h and tended to return towards control levels, particularly for fish in water with elevated Cl^- concentrations. The initial loss of Na^+ may have elicited a stress response because increases in plasma cortisol occurred at about the same time (Figs. 1 and 2). The correlation between cortisol mobilization and ion loss has been documented previously in silver-exposed fish (Webb and Wood 1998). The increase in plasma T_{amm} levels probably reflects cortisol-induced breakdown of proteins (van der Boon et al. 1997) and is characteristic of silver-induced stress. Our study showed a significant increase in plasma T_{amm} levels with only slight increases in T_{amm} excretion rates (not significant), suggesting the possibility that a relative inhibition of T_{amm} excretion may have occurred during $AgNO_3$ exposure (Table 2). As plasma T_{amm} increased, the the blood to water partial pressure gradient for NH_3 increased but this was not accompanied by a significant increase in NH_3 diffusion (i.e., T_{amm} excretion) from the fish. These results are contrary to the recent study of Webb and Wood (1998), which concluded that $AgNO_3$ exposure in relatively hard water did not affect T_{amm} excretion. The reason for this apparent inhibition of T_{amm} excretion in our experiments is unclear but may be related to differences in water chemistry compared with that of Webb and Wood (1998) or the fact that T_{amm} excretion rates were highly variable. The lack of other dramatic physiological effects is indicative of the very specific nature of Ag^+ toxicity and the relatively low level (in terms of acute toxicity) of total silver used during our exposures.

In conclusion, this study illustrates a mechanism through which water Cl^- concentration protects against the effects of waterborne $AgNO_3$ in rainbow trout by its effect on speciation, reducing the concentration of Ag^+ in the water column. A key physiological response, disruption of Na^+ balance as a result of poisoning of gill Na^+/K^+ ATPase activity, is directly related to the Ag^+ concentration of the water. Complexes of $AgCl_n^{1-n}$ do not appear to elicit a toxic physiological response but do result in accumulation of silver in the gill tissue. The results provide more evidence that speciation, particularly in relation to Cl^-, should be considered in assessing the acute toxicity of silver. Further, they suggest that inhibition of gill Na^+/K^+ ATPase activity, rather than total gill Ag burden, is the appropriate end-point on which to build future predictive models of acute silver toxicity (Bergman and Dorward-King 1997). While not precluding other Ag–gill binding data that may become available in the future, our experiments demonstrate that gill Na^+/K^+ ATPase activity is a very good predictor of gill–Ag^+ interactions and therefore provides a mechanism by which physiologically damaging interactions (gill–Ag^+) can be separated from those that are relatively innocuous (e.g., gill–AgCl). Incorporation of these interactions into acute toxicity prediction models, such as the gill receptor loading model, may prove to be successful for accurately predicting site-specific water toxicity.

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References

Allen, H.E., and Hansen, D.J. 1996. The importance of trace metal speciation to water quality criteria. Water Environ. Res. **68**: 42–54.

Audet, C., Munger, R.S., and Wood, C.M. 1988. Long-term sublethal acid exposure in rainbow trout (*Salmo gairdneri*) in soft water: effects on ion exchanges and blood chemistry. Can. J. Fish. Aquat. Sci. **45**: 1387–1398.

Babich, H., and Stotzky, G. 1983. Influence of chemical speciation on toxicity of heavy metals to the microbiota. *In* Aquatic toxicology. *Edited by* J.O. Nriagu. Adv. Envir. Sci. Tech. **13**: 1–46.

Bergman, H.L., and Dorward-King, E.J. 1997. Reassessment of metals criteria for aquatic life protection. SETAC Tech. Pub. Series. SETAC Press, Pensacola, Fla.

Boutilier, R.G., Heming, T.A., and Iwama, G.K. 1984. Physicochemical parameters for use in fish respiratory physiology. *In* Fish physiology. Vol. 10A. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, NewYork. pp. 403–440.

Bradford, M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principles of protein–dye binding. Anal. Biochem. **72**: 248–254.

Campbell, P.G.C. 1995. Interactions between trace metal and aquatic organisms: a critique of the free-ion activity model. *In* Metal speciation and bioavailability in aquatic systems. *Edited by* A. Tessier and D.R. Turner. John Wiley & Sons, New York. pp. 45–102.

Campbell, P.G.C., and Stokes, P.M. 1985. Acidification and toxicity of metals to aquatic biota. Can. J. Fish. Aquat. Sci. **42**: 2034–2049.

Davies, P.H., Goettl, J.P., Jr., and Sinley, J.R. 1978. Toxicity of silver to rainbow trout (*Salmo gairdneri*). Water Res. **12**: 113–117.

Ferguson, E.A., Leach, D.A., and Hogstrand, C. 1997. Metallothionein protects against silver blockage of Na^+/K^+ ATPase. *In* Proceedings of the 4th international conference on transport fate and effects of silver in the environment. *Edited by* A. Anders and T. Bober. University of Wisconsin Sea Grant Publication No. WISCU-W-96-001, Madison. pp. 191–196.

Galvez, F., and Wood, C.M. 1997. The relative importance of water hardness (Ca) and chloride levels in modifying the acute toxicity of silver to rainbow trout. Environ. Toxicol. Chem. **16**: 2363–2368.

Hogstrand, C., and Wood, C.M. 1998. Towards a better understanding of the bioavailability, physiology and toxicity of silver in fish: implications for water quality criteria. Environ. Toxicol. Chem. **17**: 547–561.

Hogstrand, C., Galvez, F., and Wood, C.M. 1996. Toxicity, silver accumulation and metallothionein induction in freshwater rainbow trout during exposure to different silver salts. Environ. Toxicol. Chem. **15**: 1102–1108.

Holliday, C.W. 1985. Salinity induced changes in the gill Na,K-ATPase activity in the mud fiddler crab, *Uca pugnax*. J. Exp. Zool. **233**: 199–208.

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Janes, N., and Playle, R.C. 1995. Modeling silver binding to gills of rainbow trout (*Oncorhynchus mykiss*). Environ. Toxicol. Chem. **14**: 1847–1858.

Laurén, D.J., and McDonald, D.G. 1987. Acclimation to copper by rainbow trout, *Salmo gairdneri*: physiology. Can. J. Fish. Aquat. Sci. **44**: 99–104.

LeBlanc, G.A., Mastone, J.D., Paradice, A.P., Wilson, B.F., Lockhart, H.B., and Robillard, K.A. 1984. The influence of speciation on the toxicity of silver to fathead minnow (*Pimephales promelas*). Environ. Toxicol. Chem. **3**: 37–46.

Li, J., Lock, R.A.C., Klaren, P.H.M., Swarts, H.G.P., Schuurmans-Stekhoven, F.M.A.H., Wendelaar Bonga, S.E., and Flik, G. 1996. Kinetics of Cu^{2+} inhibition of Na^+/K^+ ATPase. Toxicol. Lett. **87**: 31–38.

Morel, F.M.M., and Hering, J.G. 1993. Principles and applications of aquatic chemistry. John Wiley & Sons, New York.

Morgan, I.J., Henry, R.P., and Wood, C.M. 1997. The mechanism of acute silver nitrate toxicity in freshwater rainbow trout (*Oncorhynchus mykiss*) is inhibition of gill Na^+ and Cl^- transport. Aquat. Toxicol. **38**: 145–163.

Nebeker, A.V., McAuliffe, C.K., Mshar, R., and Stevens, D.G. 1983. Toxicity of silver to steelhead and rainbow trout, fathead minnows and *Daphnia magna*. Environ. Toxicol. Chem. **2**: 95–104.

Newman, M.C., and Jagoe, C.H. 1994. Ligands and bioavailability of metals in aquatic environments. *In* Bioavailability: physical, chemical and biological interactions. *Edited by* J.L. Hamelink, P.F. Landrum, H.L. Bergman, and W.H. Benson. CRC Press, Boca Raton, Fla. pp. 39–61.

Pagenkopf, G.K. 1983. Gill surface interaction model for the trace-metal toxicity to fishes: role of complexation, pH and water hardness. Environ. Sci. Tech. **17**: 342–347.

Pagenkopf, G.K., Russo, R.C., and Thurston, R.V. 1974. The effects of complexation on toxicity of copper to fishes. J. Fish. Res. Board Can. **31**: 462–465.

Perry, S.F. 1997. The chloride cell: structure and function in the gills of freshwater fishes. Ann. Rev. Physiol. **59**: 325–347.

Purcell, T.W., and Peters, J.J. 1998. Sources of silver in the environment. Environ. Toxicol. Chem. **17**: 539–546.

Schecher, W.D., and McAvoy, D.C. 1992. MINEQL+: a software environment for chemical equilibrium modelling. Comput. Environ. Urban Syst. **16**: 65–76.

Soivio, A., Nynlom, K., and Westman, K. 1975. A technique for repeated sampling of the blood of individual resting fish. J. Exp. Biol. **62**: 207–217.

U.S. Environmental Protection Agency (U.S. EPA). 1980. Ambient water quality criteria for silver. Final Technical Report, EPA 440-5-80-071, Washington, D.C.

van der Boon, J., van den Thillart, G.E.E.J.M., and Addink, A.D.F. 1997. The effects of cortisol on intermediary metabolism in teleost fish. Comp. Biochem. Physiol. **100A**: 47–53.

Verdouw, H., van Echteld, C.J.A., and Dekkers, E.M.J. 1978. Ammonia determination based on indophenol formation with sodium salicylate. Water Res. **12**: 399–402.

Webb, N.A., and Wood, C.M. 1998. Physiological analysis of the stress response associated with acute silver nitrate exposure in freshwater rainbow trout (*Oncorhynchus mykiss*). Environ. Toxicol. Chem. **17**: 579–588.

Wolf, K. 1963. Physiological salines for freshwater teleosts. Prog. Fish Cult. **25**: 135–140.

Wood, C.M. 1992. Flux measurements as indices of H^+ and metal effects on freshwater fish. Aquat. Toxicol. **22**: 239–264.

Wood, C.M., Hogstrand, C., Galvez, F., and Munger, R.S. 1996. The physiology of waterborne silver toxicity in freshwater rainbow trout (*Oncorhynchus mykiss*). 1. The effects of ionic Ag^+. Aquat. Toxicol. **35**: 93–109.

Wright, P.A., and Wood, C.M. 1985. An analysis of branchial ammonia excretion in the freshwater rainbow trout: effects of environmental pH change and sodium uptake blockade. J. Exp. Biol. **114**: 329–353.

Zall, D.M., Fisher, M.D., and Garner, Q.M. 1956. Photometric determination of chlorides in water. Anal. Chem. **28**: 1665–1678.

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Regimes and stock-recruitment relationships in Japanese sardine (*Sardinops melanostictus*), 1951–1995

Tokio Wada and Larry D. Jacobson

Abstract: We used reproductive success, rather than abundance or catch, to identify regimes because reproductive success responds faster to environmental changes. Peak abundance of Japanese sardine during 1951–1995 was about 1000 times higher than minimum abundance. A regime shift occurred in the early 1970s when carrying capacity (measured using spawner–recruit models) increased by about 75 times. We hypothesize that this was due to large-scale changes in the Kuroshio and Oyashio Current systems. Long-term environmental variation (regimes), interannual variability in recruitment success, and density-dependent recruitment and growth rates affected dynamics of Japanese sardine. We hypothesize that density-dependent effects on recruitment of *Sardinops* spp. are common but usually obscured in short data sets by environmental variability and measurement error. Virtual population analysis and forward-simulation modeling approaches gave similar biomass and recruitment estimates. The relationship between sardine biomass and catch per unit search time was nonlinear. Mass-at-age and biomass were correlated, and it may be possible to use mass-at-age as an abundance index. Current abundance is low, and we believe that the environment has shifted to a regime that is unfavorable for Japanese sardine.

Résumé : Nous avons retenu le succès de la reproduction, de préférence à l'abondance ou aux captures, pour déterminer les régimes, du fait que ce paramètre réagit plus vite aux changements environnementaux. L'abondance maximale de pilchard du Japon entre 1951 et 1995 était environ mille fois supérieure à l'abondance minimale. Un changement de régime s'est produit au début des années 1970, quand la capacité de port (mesurée à l'aide de modèles géniteurs–recrues) a été multipliée environ 75 fois, ce qui nous semble dû à des changements à grande échelle survenus dans les systèmes du Kuroshio et de l'Oyashio. Les variations environnementales à long terme (régimes), la variabilité interannuelle du succès du recrutement et les taux de recrutement et de croissance dépendants de la densité ont affecté la dynamique du pilchard du Japon. Nous posons que les effets dépendants de la densité qui se manifestent dans le recrutement de *Sardinops* spp. sont courants mais généralement masqués dans les séries courtes de données par la variabilité environnementale et l'erreur de mesure. L'analyse de la population virtuelle et la modélisation par simulation prospective donnaient des estimations semblables de la biomasse et du recrutement. La relation entre la biomasse de pilchard et l'indice CPUE (captures selon le temps de recherche) n'était pas linéaire. La masse selon l'âge et la biomasse étaient corrélées, et il est possible de se servir de la masse selon l'âge comme indice de l'abondance. À l'heure actuelle, l'abondance est faible, et nous pensons que l'environnement est entré dans un régime qui est défavorable au pilchard du Japon.

[Traduit par la Rédaction]

Introduction

The purpose of our paper is to estimate relationships between abundance and recruitment in the stock of Japanese sardine (*Sardinops melanostictus*; Whitehead 1985) along the Pacific coast of Japan (Fig. 1). The stock supports one of the world's largest fisheries when abundance is high (Csirke 1988).

Spawning occurs year round but peaks during February–March on southern grounds. Spawning is followed by a feeding migration to the north and offshore during summer–fall (Kondo 1980; Kuroda 1991; Watanabe et al. 1995). During winter, mature sardine return to spawning grounds, while immature fish tend to remain at wintering grounds along the central coast of Japan (Fig. 1; Kondo 1980; Hiramoto 1981). Spawning and feeding grounds differ during periods of high and low abundance (Kondo 1980; Kuroda 1988; Wada and Kashiwai 1991; Kuroda 1991; Kikuchi et al. 1992).

Nearly all catches are by purse seine (Kondo 1980; Wada 1988) in the south off Honshu and north off Hokkaido (Fig. 1). When abundance is high, fishing is between Honshu and Hokkaido (primarily summer and fall). When abundance is low, fishing is off Honshu.

Catches declined after 1988 (Table 1) following a "regime" shift (Lluch-Belda et al. 1989; Kawasaki 1991). Regimes are periods of high or low abundance. Global-scale climatic variation, such as an El Niño – Southern Oscillation

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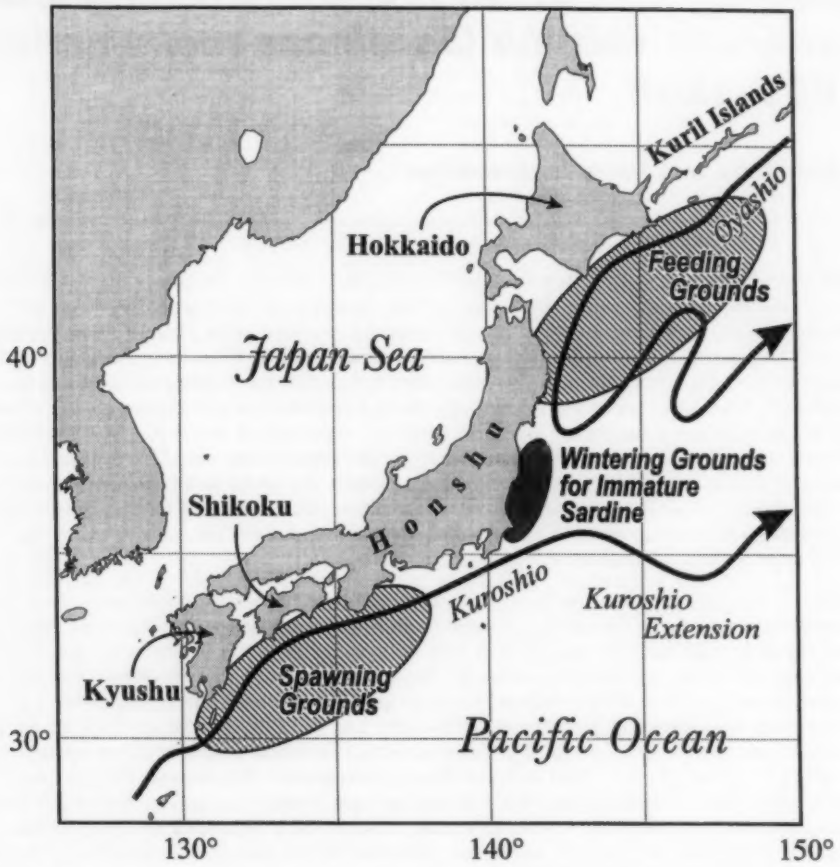
Fig. 1. Sardine habitat and fishing grounds along the Pacific coast of Japan.



(ENSO) event, is thought to cause regimes because regimes tend to occur synchronously around the world (Lluch-Belda et al. 1992; Bakun 1996). Productive regimes in Japanese sardine may be due to warmwater conditions in spawning grounds and cool-water conditions in feeding grounds following strong winter monsoons (Tomosada 1988; Hanawa 1995).

Materials and methods

Fishery and other data for Japanese sardine (Table 1) were the best available, but accuracy was poorer for early years, and data for 1995 were preliminary. Catch per unit effort (CPUE; Table 1) was catch per hour of search time (Wada and Matsumiya 1989) in the purse seine fishery off Hokkaido during 1976–1992 (Wada 1988; T. Wada, unpublished data). Annual egg production data (eggs·year^{-1}) (Table 1) were from annual ichthyoplankton surveys. The recruitment index was CPUE (t·shot^{-1}) in the winter purse seine fishery off the Joban and Boso areas of central Honshu (Fig. 1). The fishery takes immature (mostly age-1 with small amounts of age-2) sardine on their wintering grounds during January–March. We used the index as an index of recruitment at age-0 during December of the previous year.

Virtual population analysis model

We used virtual population analysis (VPA; Megrey 1989) and the ADAPT procedure (Gavaris 1988, as implemented by Jacobson 1993) to estimate sardine abundance and recruitment during recent years (1976–1995) with catch-at-age data available. Crude variance estimates for parameters were estimated from the Hessian matrix (Jacobson et al. 1994*a*). The assumed natural mortality rate (M = 0.4·year^{-1}) was based on a statistical relationship between longevity and mortality rates (Tanaka 1960; Kawai 1987). Fishing mortality rates for sardine age-4 and age-5+ were assumed equal and calculated by "linking cohorts" (Prager and MacCall 1988). Biomass and abundance estimates (including recruitments) were for the middle of June, the end of the major spawning season for Japanese sardine.

Fishing mortality rates for sardine during the terminal year and other parameters in the VPA (see below) were chosen to minimize the sum of squares:

$$(1) \qquad \Xi = \sum_{i=1}^{3} \sum_{y=1}^{n_i} \ln\left(I_{i,y}/\hat{I}_{i,y}\right)^2$$

where $I_{i,y}$ was the observed abundance index (with n_i observations) and $\hat{I}_{i,y}$ was the abundance predicted by the model (hats "^" indicate predicted values). Abundance indices were predicted as follows:

$$(2) \qquad \hat{I}_{i,y} = Q_{i,y}\left(\sum_{a=0}^{5+} A_{y,a}\, s_{i,y,a}\right)^{\gamma}$$

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where $Q_{i,y}$ was a scaling parameter, $A_{y,a}$ was sardine abundance at age a when the survey was conducted, and $s_{i,y,a}$ was a selectivity parameter measuring the age-specific contribution of sardine to the index. Abundance was either numbers of fish ($N_{y,a}$) or biomass ($B_{y,a} = N_{y,a}w_{y,a}$ where $w_{y,a}$ was a mean mass-at-age in the fishery during June).

Selectivities were relative measures scaled to a maximum value of one (see below). Scaling parameters ($Q_{i,y}$) for sardine abundance data were assumed to be constant over time unless there was evidence to the contrary (see below). The exponent (γ) was one unless the relationship between abundance of sardine and an index proved to be nonlinear (MacCall 1976).

Selectivity parameters for sardine egg production data were estimates of average annual population fecundity-at-age (eggs per year). Average annual population fecundity-at-age in clupeoid fishes like sardine (Macewicz et al. 1996; Lo et al. 1996) and northern anchovies (e.g., *Engraulis mordax*; Lasker 1985) is the product of the age-specific sex ratio, maturity, batch size (eggs per batch), spawning frequency during the spawning season (batches per day), and length of the spawning season (days spawning per year). We approximated annual fecundity-at-age for Japanese sardine as the product of age-specific maturity and batch fecundity. Lacking information, we assumed that sex ratio, spawning frequency, and duration of spawning were the same for all age groups.

Maturity and batch fecundity-at-age were estimated based on mean mass-at-age in the fishery, a maturity-at-length relationship for Pacific sardine off California (*Sardinops sagax*; Macewicz et al. 1996), a batch fecundity-at-length relationship for Japanese sardine (Watanabe 1988), and a length–weight relationship for Japanese sardine (Hiramoto 1981). To preserve information about relative changes in population fecundity from year to year, we scaled fecundity estimates so that the largest value in all years was equal to one.

Average annual population fecundity-at-age probably varied over time in Japanese sardine because of changes in growth (Wada 1988) and other density-dependent or environmental factors. Changes in growth were likely particularly important because maturity, batch size, and spawning frequency change rapidly as Japanese sardine grow. Fortunately, we were able to accommodate variability in average annual population fecundity-at-age due to changes in growth by linking maturity and batch size-at-age in our VPA model to mean weights in the fishery. In addition, by rescaling the selectivity parameters for egg production so that the largest value in all years was equal to one, we were able to accommodate year to year changes in population fecundity due to changes in age structure.

Selectivities for CPUE data for sardine in the Hokkaido fishery were

$$(3) \qquad S_{\mathrm{CPUE},y,a} = \frac{f_{y,a}}{f_{y,4}}$$

where $f_{y,a} = \upsilon_{y,a}F_{y,a}$, $\upsilon_{y,a}$ was the fraction of the total catch-at-age a from the Hokkaido fishery, and $F_{y,a}$ was estimated by VPA.

Selectivity of age-0 sardine (age-1 in year $y + 1$) was assumed to be one for the recruitment index and selectivity for 1 year olds (age-2 in year $y + 1$) was estimated in the model. Selectivities for older ages were zero.

Spreadsheet model

We used a simple age-structured spreadsheet model to estimate sardine biomass during early years (1951–1975) with no catch-at-age data. The spreadsheet model used a forward-simulation approach (Methot 1990; Jacobson et al. 1994*a*) and was fit to egg production data, the only abundance index available for early years. The initial year of the spreadsheet model was 1946, and the terminal year was 1981.

Parameters estimated in the spreadsheet model included recruit-

Table 1. Catch (aggregated by January–December calendar years) and abundance indices for sardine along the Pacific coast of Japan during 1951–1995.

Year	Catch (t, × 1000)	Egg production (eggs·year^{-1}, × 10^{12})	CPUE (t·h^{-1})	Recruitment index (t·shot^{-1})
1951	37	26	—	—
1952	23	19	—	—
1953	22	12	—	—
1954	13	22	—	—
1955	11	22	—	—
1956	19	22	—	—
1957	20	26	—	—
1958	18	11	—	—
1959	18	10	—	—
1960	19	45	—	—
1961	101	221	—	—
1962	96	96	—	—
1963	44	14	—	—
1964	8	14	—	—
1965	4	17	—	—
1966	3	4	—	—
1967	6	5	—	—
1968	15	2	—	—
1969	17	4	—	—
1970	15	1	—	—
1971	49	2	—	—
1972	39	17	—	—
1973	235	22	—	—
1974	243	153	—	—
1975	408	210	—	—
1976	784	271	25	7
1977	1109	318	41	27
1978	1183	1444	36	19
1979	1253	444	60	5
1980	1679	937	49	82
1981	2460	1338	62	66
1982	3037	1242	94	11
1983	3495	853	106	80
1984	3786	1839	117	67
1985	3356	2081	81	100
1986	3766	8985	79	72
1987	3699	1860	116	65
1988	3902	3784	104	2
1989	3313	3897	68	8
1990	2781	6529	71	1
1991	2224	3665	81	1
1992	1224	1669	22	49
1993	720	1581	0	6
1994	432	327	0	3
1995	271	180	0	1

Note: Data for 1951–1977 are from Watanabe (1983); 1978–1986, from Mori et al. (1988); 1987–1988, from Kikuchi and Konishi (1990); 1989–1990, from Ishida and Kikuchi (1992); 1991–1993, from Zenatani et al. (1995); and 1994–1995, from National Research Institute of Fisheries Science (unpublished data).

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ments (R_y), a scaling parameter for egg production data (Q_{egg}, assumed constant over time) and spawner–recruit parameters (see below). Recruitments during 1946–1950 (which determined abundance of sardine age-2+ during 1951, the first year with egg production data) were assumed constant. Recruitments during 1951–1981 were estimated individually.

Population dynamics were modeled using Pope's (1972) cohort analysis. Catch-at-age ($c_{y,a}$ in numbers of fish) was

$$(4) \qquad c_{y,a} = \frac{\bar{s}_a X_y U_y}{\bar{w}_a}$$

where $\bar{s}_a$ was average selectivity for sardine in the Honshu fishery during 1976–1981 (estimated from VPA results), and $\bar{w}_a$ was average mass-at-age during 1976–1981 (from the VPA data). X_y was exploitable biomass on 1 July:

$$(5) \qquad X_y = \sum_{a=0}^{5+} \bar{s}_a B_{y,a} e^{-M/2}$$

U_y was the fraction of the exploitable biomass taken by the fishery:

$$(6) \qquad U_y = \frac{L_y}{X_y}$$

where L_y was total landings.

Preliminary runs indicated that recruitment estimates for sardine from the spreadsheet model were too variable (Jacobson et al. 1994*a*). To get better recruitment estimates for Japanese sardine during early years, we used a recruitment constraint based on the variance in log reproductive success ($\sigma^2 = 1.9$) estimated by fitting a linearized Ricker (1975) spawner–recruit model to "data" from the VPA. The objective function for the final spreadsheet model, including the spawner–recruit constraint, was

$$(7) \qquad Y = \sum_{y=1951}^{1981} \ln(I_{egg,y}/\hat{I}_{egg,y})^2 + 0.001 \times \sum_{y=1951}^{1981} \ln(\tilde{R}_y / \hat{R}_y)^2 + 1000 \ln(\tilde{\sigma}^2 / \sigma^2)$$

where $\tilde{R}_y$ and $\tilde{\sigma}^2$ are estimates from the Ricker model in the spreadsheet. The large weight (1000) for the right-hand term in eq. 7 means that the recruitment estimates from the spreadsheet model were, as a group, constrained to have exactly the same variance as estimated from the VPA data (Jacobson et al. 1994*a*). A very low weight (0.001) was used for the individual spawner–recruit predictions from the Ricker model (middle term in eq. 7) because we wanted to base recruitment estimates from the spreadsheet model on egg production and catch data and the variance constraint but not on predicted recruitments from the Ricker model. Thus, predicted values from the spawner–recruit model were intended to have minimal effects on the final recruitment estimates. In effect, the Ricker curve (middle term in eq. 7) was included in the spreadsheet model only so that variance around the curve ($\tilde{\sigma}^2$) could be calculated and compared with the target value (σ^2).

Results and discussion

Residual plots for preliminary VPA runs indicated that the relationship between sardine abundance and CPUE in the Hokkaido fishery was nonlinear. We estimated an exponent parameter ($\gamma = 0.36$, CV = 59%) in final runs to improve fit to the CPUE data.

Preliminary VPA runs consistently overestimated egg production prior to 1984 and underestimated egg production subsequently. Lack of fit to egg production data may have been from a change in survey pattern in 1984, a shift in spawning grounds (Kuroda 1988; Kikuchi et al. 1992), or changes in age-specific reproductive output of Japanese sardine, although our approach to estimating selectivities for egg production data reduced this potential problem (see earlier).

Unfortunately, hypotheses about lack of fit to egg production data in preliminary VPA runs were confounded and impossible to resolve using available data. To address all possibilities, we modified the model so that the scaling parameter for egg production varied over time:

$$(8) \qquad Q_{egg,y} = e^{\varsigma + \tau D_y}$$

where ς and τ were estimated in the model and D_y was a dummy variable equal to zero for 1976–1983 and 1994–1995 and one for years 1984–1993. The estimate ($\tau = 1.2$, CV = 37%) was statistically significant from zero and may imply a reduction in survey coverage because of changes in the survey pattern or a shift in spawning grounds of about $1 - 1/e^{1.2} = 70\%$ during 1984–1993.

We were not able to estimate age-specific fishing mortality rates for sardine during 1995 directly in the VPA, a typical problem with abundance data that are not age specific (e.g., Jacobson et al. 1994*b*). We therefore set terminal fishing mortality rates equal to the product of average age-specific selectivities for the southern fishery around Honshu during 1990–1994 and a fishing mortality rate estimated in the model.

Results for 1976–1981 from the spreadsheet and VPA models were similar (Fig. 2) indicating that biomass and recruitment estimates from the two modeling approaches were comparable. VPA estimates used in the spreadsheet model seemed reasonable and are summarized below.

Age	Average relative fecundity	Average mass at age (kg)	Average selectivity in Honshu fishery
0	0.00	0.0037	0.23
1	0.27	0.056	0.42
2	0.62	0.090	0.43
3	0.80	0.113	0.67
4	0.92	0.127	0.81
5+	1.00	0.136	1.00

Sensitivity analyses (see below) showed that our biomass and recruitment estimates for Japanese sardine were sensitive to the structure of the spreadsheet model (i.e., the constraint on recruitment variance) but not to small changes in weights used in the objective function (eq. 7). Hundredfold changes to the weight on recruitment variance (1000 to 10) and the weight for spawner–recruit predictions (0.001 to 0.1) changed estimated average biomass during 1976–1981 by 6% or less and estimated average recruitment by 12% or less. Biomass estimates were less sensitive than recruitment estimates, and the weight used on the variance was more important than the weight used on predictions from the Ricker curve.

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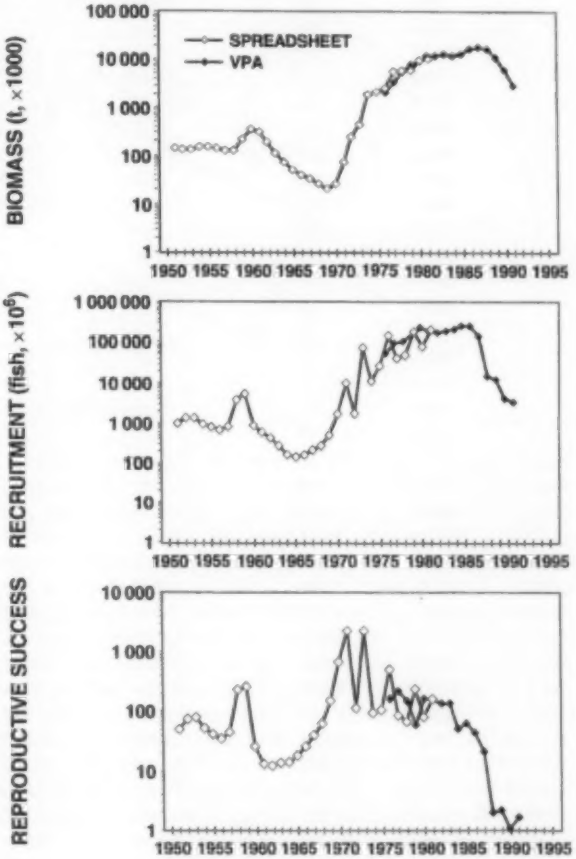
Weight on recruitment variance	Weight on Ricker curve predictions			
	0.001	0.1	10	1000
% Change in estimated average biomass during 1976–1981				
0.001	30	0	–7	21
0.1	25	0	–7	18
10	6	0	–16	–6
1000	0*	0	–8	–11
% Change in estimated average recruitment during 1976–1981				
0.001	53	0	–6	49
0.1	46	0	–7	43
10	12	0	–33	–15
1000	0*	0	–16	–23

*Default weights.

Fig. 2. Sardine biomass (upper panel: age-0+, t (× 1000) during mid-June to July), recruitment (middle panel: age-0 fish (× 10^{12}) on 1 July), and reproductive success (lower panel: recruits per unit annual egg production) during 1951–1991. Estimates for 1951–1981 were from a spreadsheet model. Estimates for 1976–1991 were from VPA.



Population dynamics

Biomass, recruitment, and reproductive success of Japanese sardine (Table 2, Fig. 2) varied 1000-fold during 1951–1995. The "recruitment failure" (Watanabe et al. 1995) during 1988–1991 was dramatic by recent standards, but sardine recruitment during 1988–1991 did not decline as low as at any time before 1971.

We calculated an annual index of exploitation, Z_y, for Japanese sardine based on cohort analysis (Pope 1972):

$$(9) \qquad Z_y = \frac{L_y}{B_t e^{-M/2}}$$

The exploitation index (Table 2) averaged 18%·year^{-1} prior to 1961 and increased to 36%·year^{-1} during 1961–1970.

Mass-at-age data for Japanese sardine might be useful as an index of abundance. Wada (1988) and Wada et al. (1995) found negative correlations between abundance and individual growth of Japanese sardine. In this study, correlations (ρ = –0.51, –0.86, –0.84, –0.70, and –0.53) between mass at age-1 to age-5+ and sardine biomass estimates[2] from VPA were also negative and statistically significant ($p < 0.05$).

Spawner–recruit analysis

Based on results for Japanese (see below) and Pacific sardine off California (Jacobson and MacCall 1995), we hypothesize that density-dependent effects on recruitment typically exist for *Sardinops* spp. but can only be measured using long time series of data with large (1000-fold) changes in abundance (Hilborn and Walters 1992).

We used spawner–recruit models and analysis of variance to test six hypotheses about regime effects on reproductive success of sardine. The models were fit by linear regression of log reproductive success (ln R_y/E_y) on log egg production (ln E_y). Intercept parameters in our spawner–recruit models tested hypotheses about regimes and slope parameters tested hypotheses about density-dependent effects. We excluded the last years (1992–1995) of spawner–recruit data from regression analyses because they were unreliable (Megrey 1989). The logarithm of egg production (predicted values for the egg production index from our models) was used as the independent variable because of the extreme range in egg production by Japanese sardine.

We used reproductive success, rather than changes in abundance or catch (e.g., Lluch-Belda et al. 1989), to identify regimes because it is an important part of biological production and can change more quickly in response to environmental variability. Two regimes (unfavorable during 1951–1970 and 1988–1991 and favorable during 1971–1987) were assumed (Fig. 3).

The best hypothesis and model for reproductive success in Japanese sardine included long-term environmental effects (an intercept parameter for each regime) and a density-dependent effect (slope parameter). Parameters were as follows:

[2] Average mass-at-age during 1976–1995 were used to calculate biomass for correlation analyses because results would be tend to be biased if annual mass-at-age data were included in both variables.

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Table 2. Biomass, recruitment, and exploitation index estimates for Japanese sardine during 1951–1995.

Year	0+ Biomass (t, × 1000)	1+ Biomass (t, × 1000)	Annual egg production (eggs·year^{-1}, × 10^{12})	Recruits (fish, × 10^6)	Exploitation index
1951	146	143	20	1 001	0.22
1952	138	134	18	1 362	0.15
1953	143	138	17	1 373	0.14
1954	156	152	18	953	0.08
1955	157	154	19	814	0.07
1956	147	144	20	700	0.12
1957	130	127	18	831	0.14
1958	131	117	16	3 744	0.13
1959	233	214	20	5 180	0.07
1960	376	373	34	897	0.05
1961	326	323	46	611	0.27
1962	206	204	36	448	0.38
1963	117	116	21	285	0.32
1964	77	77	12	171	0.10
1965	53	53	8	148	0.07
1966	43	43	6	168	0.07
1967	36	35	5	218	0.16
1968	28	27	5	285	0.43
1969	22	21	3	524	0.55
1970	27	22	3	1 711	0.43
1971	76	46	4	9 570	0.49
1972	263	256	15	1 749	0.14
1973	457	230	32	70 870	0.41
1974	1 976	1 937	113	10 728	0.12
1975	2 205	2 114	240	25 491	0.17
1976	2 186	1 992	313	51 444	0.38
1977	3 436	3 061	454	99 467	0.35
1978	5 669	5 279	677	103 501	0.24
1979	8 045	7 799	1087	65 071	0.18
1980	9 695	8 824	1399	230 860	0.20
1981	11 857	11 143	1182	189 572	0.23
1982	12 528	11 882	1226	171 652	0.27
1983	12 863	12 140	1372	191 689	0.30
1984	12 610	11 792	4194	216 795	0.32
1985	13 330	12 387	3836	249 815	0.28
1986	16 724	15 728	5917	264 435	0.25
1987	18 377	17 833	6702	143 803	0.23
1988	16 355	16 300	7310	14 623	0.27
1989	10 818	10 771	5716	12 392	0.33
1990	6 288	6 273	3664	3 989	0.45
1991	2 938	2 925	1958	3 321	0.66
1992	925	847	675	20 591	0.90
1993	778	724	461	14 506	0.74
1994	739	680	107	15 767	0.55
1995	997	948	139	13 053	0.30

Note: Estimates for 1951–1975 are for 1 July from a spreadsheet model. Estimates for 1976–1995 are for mid-June from virtual population analysis (VPA). Recruits are numbers of age-0 sardine on 1 June. Estimates for 1992–1995 are not reliable.

Parameter	Estimate	SE
Intercept during unfavorable regime (κ_U)	5.72	0.436
Intercept during favorable regime (κ_F)	8.75	0.782
Density-dependent slope (π)	–0.701	0.128

and the variance of residuals for log reproductive success was 1.27 (R^2 = 44%, 38 df). For example, predicted recruits for an egg production of 200 × 10^{12} during 1951–1970 or 1988–1991 (unfavorable regime) would be $200e^{5.72-0.701\ln(200)}$ = 1.4 × 10^9 age-0 sardine or $200e^{8.75-0.701\ln(200)}$ = 31 × 10^9 age-0 sardine during 1971–1987 (favorable regime).

Density-dependent effects on sardine egg production on reproductive success were similar in different regimes. A model with a separate slope parameters for each regime gave similar predicted values and was not significantly better than our best model with a single slope parameter.

According to our best spawner–recruit model for Japanese sardine:

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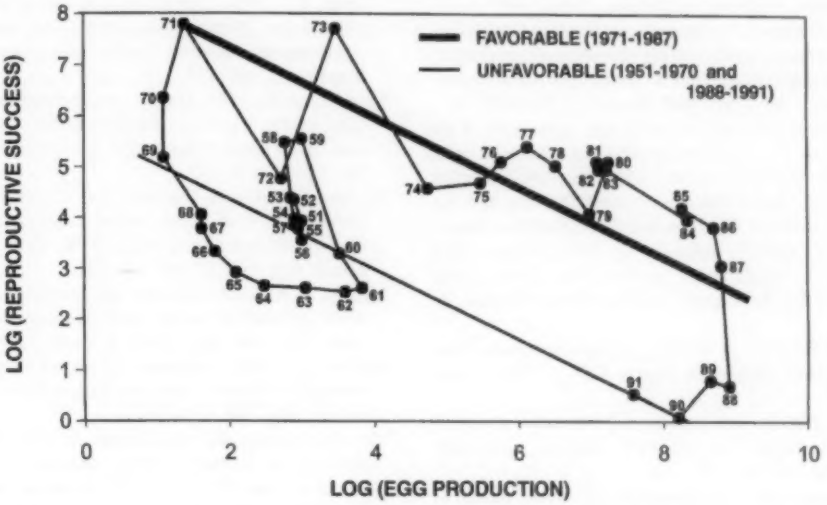
Fig. 3. Log reproductive success (recruits per unit annual egg production) versus log annual egg production for Japanese sardine during 1951–1991 with predicted values from the best fitted regression model (see text) for favorable (upper line) and unfavorable (lower line) regimes.



$$R = Ee^{\kappa+\pi\ln(E)} \quad (10)$$

where E is egg production and R is recruits. If egg production over the lifetime of one recruit in an unfished stock at carrying capacity is μ, then:

$$E^* = \mu E^{1+\pi} e^{\kappa} \quad (11)$$

where E^* is lifetime egg production by all of the recruits in a year-class. With no fishing and at equilibrium, carrying capacity (in eggs) is

$$E^* = E = \frac{e^{-\kappa/\pi}}{\mu} \quad (12)$$

Thus, carrying capacity (in units of eggs per year) for Japanese sardine is proportional to $e^{-\kappa/\pi}$. Based on our regression parameter estimates, the carrying capacity for Japanese sardine during the favorable regime of 1971–1995 was about 75 times greater than carrying capacity during 1951–1970 or 1988–1991. This is likely an underestimate of the change in carrying capacity given the 1000-fold change in biomass (see above). The cause of the increase during the early 1970s is unknown, but its magnitude indicates large, and hopefully visible, changes in the physical environment of sardine in the Kuroshio and Oyashio Current systems off the coast of Japan.

Density-dependent effects on recruitment of Japanese sardine make the potential for recruitment overfishing (Ricker 1975) in Japanese sardine plausible. California sardine is sensitive to fishing pressure during periods of unfavorable environmental conditions (Barnes et al. 1992; Jacobson and MacCall 1995; Deriso et al. 1996).

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References

Bakun, A. 1996. Patterns in the ocean. California Sea Grant/CIB, San Diego.

Barnes, J.T., Jacobson, L.D., MacCall, A.D., and Wolf, P. 1992. Recent population trends and abundance estimates for sardine (*Sardinops sagax*). Calif. Coop. Oceanic Fish. Invest. Rep. No. 33. pp. 60–75.

Csirke, J. 1988. Small shoaling pelagic fish stocks. *In* Fish population dynamics. 2nd. ed. *Edited by* J.A. Gulland. John Wiley & Sons, New York. pp. 271–302.

Deriso, R.B., Barnes, J.T., Jacobson, L.D., and Arenas, P.R. 1996. Catch-at-age analysis for Pacific sardine (*Sardinops sagax*), 1983–1995. Calif. Coop. Oceanic Fish. Invest. Rep. No. 37. pp. 175–187.

Gavaris, S. 1988. An adaptive framework for the estimation of population size. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. No. 88/29.

Hanawa, K. 1995. Southward penetration of Oyashio water system and the winter time condition of mid latitude westerlies over the

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north Pacific. (In Japanese). Bull. Hokkaido Natl. Fish. Res. Inst. **59**: 103–120.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Routledge, Chapman & Hall Inc., New York.

Hiramoto, K. 1981. Studies on the growth and life cycle of the Japanese sardine *Sardinops melanostictus* (Temminck et Schlegel) in its Pacific sub-population found in Joban and Boso regions. (In Japanese). Bull. Chiba Pref. Fish. Exp. Stn. **39**: 1–70.

Ishida, M., and Kikuchi, H. 1992. Monthly egg production of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1989 through December 1990. (In Japanese). Nansei National Research Institute, and National Research Institute of Fisheries Science, Yokohama, Japan.

Jacobson, L.D. 1993. ADEPT: software for VPA analysis using Gavaris's procedure. Admin. Rep. No. LJ-93-02. National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, Calif.

Jacobson, L.D., and MacCall, A.D. 1995. Stock–recruitment models for Pacific sardine (*Sardinops sagax*). Can. J. Fish. Aquat. Sci. **52**: 566–577.

Jacobson, L.D., Lo, N.C.H., and Barnes, J.T. 1994*a*. A biomass-based assessment model for northern anchovy, *Engraulis mordax*. Fish. Bull. U.S. **92**: 711–724.

Jacobson, L.D., Konno, E.S., and Pertierra, J.P. 1994*b*. Status of Pacific mackerel and trends in biomass. Calif. Coop. Oceanic Fish. Invest. Rep. No. 35. pp. 36–39.

Kawai, T. 1987. A study on variability of marine teleost resources from a viewpoint of comparative ecology. (In Japanese.) Bull. Tokai Reg. Fish. Res. Lab. **122**: 49–127.

Kawasaki, K. 1991. Long-term variability in the pelagic fish populations. *In* Long term variability of pelagic fish populations and their environments. *Edited by* T. Kawasaki, S. Tanaka, and Y. Toba. Pergamon Press, London. pp. 47–60.

Kikuchi, H., and Konishi, Y. 1990. Monthly egg productions of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1987 through December, 1988. (In Japanese.) Nansei National Research Institute, and National Research Institute of Fisheries Science, Yokohama, Japan.

Kikuchi, H., Mori, K., and Nakata, K. 1992. Offshore shift of the spawning ground of Japanese sardine (in the waters east of Cape Shionomisaki, along the Pacific coast of central Japan). (In Japanese.) Bull. Jpn. Soc. Sci. Fish. **58**: 427–432.

Kondo, K. 1980. The recovery of the Japanese sardine—the biological basis of stock-size fluctuation. Rapp. P.-V. Reun. Cons. Int. Explor. Mer, **177**: 332–354.

Kuroda, K. 1988. Yearly changes of the main spawning grounds of the sardine, *Sardinops melanostictus* (T. et. S.) in the waters along the Pacific coast of southern Japan. (In Japanese.) Bull. Jpn. Soc. Fish. Oceanogr. **52**: 289–296.

Kuroda, K. 1991. Studies on the recruitment process focussing on the early life history of the Japanese sardine, *Sardinops melanostictus* (Schlegel). (In Japanese.) Bull. Natl. Res. Inst. Fish. Soc. **3**: 25–278.

Lasker, R. (*Editor*). 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*). NOAA Tech. Rep. NMFS No. 36.

Lluch-Belda, D., Crawford, R.J.M., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A., and Smith, P.E. 1989. World wide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. **8**: 195–205.

Lluch-Belda, D., Hernandez-Vazquez, S., Lluch-Cota, D.B., Salinas-Zavala, C.A., and Schwartzlose, R.A. 1992. The recovery of the California sardine as related to global change. Calif. Coop. Oceanic Fish. Invest. Rep. No. 33. pp. 50–59.

Lo, N.C.H., Green-Ruiz, Y.A, Cervantes, M.J., Moser, H.G., and Lynn, R.J. 1996. Egg production and spawning biomass of Pacific sardine (*Sardinops sagax*) in 1994, determined by the daily egg production method. Calif. Coop. Oceanic Fish. Invest. Rep. No. 37. pp. 160–174.

MacCall, A.D. 1976. Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. Calif. Coop. Oceanic Fish. Invest. Rep. No. 18. pp. 136–148.

Macewicz, B., Castro-Gonzalez, J.J., Cotero-Altamirano, C.E., and Hunter, J.R. 1996. Adult reproductive parameters of Pacific sardine (*Sardinops sagax*) during 1994. Calif. Coop. Oceanic Fish. Invest. Rep. No. 37. pp. 140–151.

Megrey, B.A. 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. Am. Fish. Soc. Symp. **6**: 8–48.

Methot, R.D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. Int. North Pac. Fish. Comm. Bull. **50**: 259–277.

Mori, K., Kuroda, K., and Konishi, Y. 1988. Monthly egg productions of the Japanese sardine, anchovy, and mackerels off the southern coast of Japan by egg censuses: January, 1978 through December, 1986. (In Japanese.) Tokai Regional Fisheries Research Laboratory, Tokyo, Japan.

Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. Int. Comm. Northwest Atl. Fish. Res. Bull. **9**: 65–74.

Prager, M.H., and MacCall, A.D. 1988. Sensitivities and variances of virtual population analysis as applied to the mackerel, *Scomber japonicus*. Can. J. Fish. Aquat. Sci. **45**: 539–547.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Tanaka, S. 1960. Studies on the dynamics and management of fish populations. (In Japanese.) Bull. Tokai. Reg. Fish. Res. Lab. **28**: 1–200.

Tomosada, A. 1988. Long-term variation of sardine catch and temperature. (In Japanese.) Bull. Tokai Reg. Fish. Res. Lab. **126**: 1–9.

Wada, T. 1988. Population dynamics on Japanese sardine, *Sardinops melanostictus*, caught by the domestic purse seine fishery in the waters off the coast of southeastern Hokkaido. Bull. Hokkaido Reg. Fish. Res. Lab. **52**: 1–138.

Wada, T., and Kashiwai, K. 1991. Changes in growth and feeding ground with fluctuation in stock abundance. *In* Long-term variability of pelagic fish populations and their environments. *Edited by* T. Kawasaki, S. Tanaka, and Y. Toba. Pergamon Press, London. pp. 181–190

Wada, T., and Matsumiya, Y. 1989. Abundance index in purse seine fishery with searching time. Bull. Jpn. Soc. Sci. Fish. **56**: 725–728.

Wada, T., Matsubara, T., Matsumiya, Y., and Koizumi, N. 1995. Influence of environment on stock fluctuations of Japanese sardine, *Sardinops melanostictus*. *In* Climate Change and Northern Fish Populations. Proceedings of a Symposium, 19–24 Oct. 1992, Victoria, B.C. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 387–394

Watanabe, T. 1983. Stock assessment of common mackerel and Japanese sardine along the Pacific coast of Japan by spawning survey. FAO Fish. Rep. No. 291. pp. 57–81.

Watanabe, T. 1988. Some aspects of stock assessment for Japanese sardine—method for estimating spawning biomass based on egg

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census. (In Japanese.) *In* Proceedings of the 19th (1986) Pelagic Fish Symposium, 15–16 Dec. 1986, Tokyo. Japan Scientific Council on the Fisheries Resources, Fisheries Agency. pp. 73–88.

Watanabe, Y., Zenitani, H., and Kimura, R. 1995. Population decline of the Japanese sardine *Sardinops melanostictus* owing to recruitment failure. Can. J. Fish. Aquat. Sci. **52**: 1609–1616.

Whitehead, J.P. 1985. FAO species catalogue. Clupeoid fishes of the world. An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. Part 1—Chirocentridae, Clupeidae and Pristigasteridae. FAO Fish. Synop. No. 125 7(1).

Zenitani, H., Ishida, M., Konishi, Y., Goto, T., Watanabe, Y., and Kimura, R. 1995. Distribution of eggs and larvae of pelagic fish species around Japan. (In Japanese). National Research Institute of Fisheries Science, Yokohama, Japan.

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Changes to the runoff of Canadian ecozones under a doubled CO_2 atmosphere

Thomas A. Clair, James Ehrman, and Kaz Higuchi

Abstract: Increases in atmospheric greenhouse gases may change the hydrology of a number of Canada's regions. This will have an impact on aquatic and wetland ecosystems as well as municipal, industrial, and power generation uses. It is thus important to get an estimate of the potential changes to the Canadian hydrological cycle in order to make intelligent decisions concerning mitigation factors that society may be forced to undertake. We divided Canada into ecoclimatologically similar regions called "ecozones." We developed two month-stepped temperature–precipitation–runoff models for the country using an artificial intelligence neural network (ANN) approach. We modified input temperature and precipitation variables in the ANN models to match those predicted by the Canadian Climate Centre General Circulation Model II for a doubled CO_2 atmosphere and calculated new monthly equilibrium runoff predictions. Our results predict that much of Canada will experience higher annual runoff than is currently the case. The timing of runoff will change significantly in a number of the ecozones, as we show that in many regions, peak runoff will occur approximately 1 month earlier than is currently the case. The ANN model did not work as well for basins in the Prairie ecozone, as we could not develop a good model with data from regulated rivers.

Résumé : L'accroissement des concentrations atmosphériques de gaz à effet de serre peut modifier l'hydrologie de certaines régions du Canada. Cela aura un impact sur les écosystèmes aquatiques et sur les milieux humides, sur les utilisations municipales et industrielles des eaux de même que sur la production d'électricité. Il est donc important de disposer d'une estimation des changements potentiels du cycle hydrologique canadien afin de pouvoir prendre des décisions éclairées concernant les mesures d'atténuation que la société peut se trouver obligée de prendre. Nous avons divisé le Canada en régions dans lesquelles on trouve des conditions éco-climatologiques relativement uniformes, appelées « écozones ». Nous avons élaboré des modèles température–précipitation–ruissellement à pas de temps de deux mois pour le pays en utilisant une approche fondée sur l'intelligence artificielle (réseau neuronal, modèles ANN). Nous avons modifié les variables d'entrée de température et de précipitation dans les modèles ANN pour les faire correspondre à celles prévues par le modèle de circulation générale II du Centre climatologique canadien pour une atmosphère à double CO_2, et calculé de nouvelles prévisions mensuelles du ruissellement d'équilibre. Nos résultats prévoient qu'une bonne partie du Canada connaîtra un ruissellement annuel plus important qu'actuellement. Il y aura modification temporelle importante du ruissellement dans certaines écozones; en effet, dans bon nombre de régions, le ruissellement maximal se produira environ un mois plus tôt qu'actuellement. Le modèle ANN ne donnait pas d'aussi bons résultats dans le cas de bassins de l'écozone des Prairies, étant donné que nous ne pouvions pas élaborer un bon modèle avec des données provenant de cours d'eau régularisés.

[Traduit par la Rédaction]

Introduction

It is most likely that the planet's climate will change with increasing levels of atmospheric concentrations of CO_2 (Manabe et al. 1991; Boer et al. 1992; Russel et al. 1995). Humanity's increasing dependance on the use of fossil fuels is creating conditions that will have important ramifications to the hydrological cycle of large parts of North America. Changes in the patterns and amounts of water moving through streams, rivers, and lakes caused by a modified climate will have implications for aquatic ecosystems as well as on human water uses. For example, Eaton and Scheller (1996), using the Canadian Climate Centre (CCC) General Circulation Model (GCM), suggested that in the United States, reductions of up to 50% of both cold and warm water habitats would occur under a doubling of atmospheric CO_2 ($\times 2$ CO_2) scenario. Stemberger et al. (1996) also showed that zooplankton communities are influenced by air temperatures, with cooler conditions in the northeastern United States being correlated with higher species diversities.

Changes in climate will also affect other components of aquatic ecosystems. For example, Schindler et al. (1996) showed that warmer and drier hydrological conditions will reduce dissolved organic carbon concentrations in lakes, exposing biota to increased UV-B radiation. Changes to water amounts and seasonal distributions will also have impacts on domestic water supplies, flood forecasting and control, and hydroelectric structures and planning (Loaiciga et al. 1996; Frederick and Major 1997).

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Developing water resource predictions for a country as large as Canada is a difficult task. A number of different modeling approaches exist, but most of them require extensive data sets and are difficult to transport between basins. Recently, Clair and Ehrman (1996) used neural networks, an artificial intelligence approach to predict how water and dissolved organic carbon flows in rivers of Atlantic Canada would vary under a range of climate change scenarios. In practice, neural networks are especially useful for mapping problems that are tolerant of high error rates and have abundant data available but to which hard and fast rules (e.g., cause–effect models) cannot be easily applied (Rumelhardt and McClelland 1986).

Neural networks are a relatively new way of looking at data. The approach is a mathematically valid pattern recognition technique that produces complex algorithms describing the interrelationship between a number of input variables and a related output (Rumelhardt and McClelland 1986). The model inputs need not be independent of each other, so that correlated inputs can be used (e.g., mean and maximum daily temperatures), and the model itself decides if one is more important than the other.

Clair and Ehrman (1998) further refined their initial approach to use monthly climate inputs as well as basin geographical features to produce predictions of monthly discharge and dissolved carbon fluxes from individual basins. We then varied precipitation and temperature inputs to the validated hydrological models to match those predicted by three different climate scenarios to see how water and carbon flows might change seasonally under a new climate regime. This approach worked well enough to encourage us to extend the approach to study changes in runoff in the rest of Canada in order to see how water resources would change with a changing temperature and precipitation regime.

We define runoff as a basin's stream flow divided by its surface area. This value integrates a number of processes, such as overland flow from snowmelt and heavy rainstorms, subsurface flow from shallow soils (often referred to as interflow), and groundwater inflow to streams and rivers. Although river and stream flow are usually measured in cubic metres per second, normalizing river runoff by the surface area and manipulating the time factor, we produce values related in millimetres per time period (in our case, per month). There are a number of advantages to this normalization. First, runoff can be directly compared with precipitation, which is usually reported in millimetres per time period. Second, and very important to this study, it allows easy comparisons of the hydrology of basins with greatly varying sizes. Two geographically close basins but with widely different areas should produce roughly similar runoff values, allowing for a better comparison.

Because of the importance of water to Canadian ecosystems and economy, we felt that it was important to see how predicted changes in climate under a CO_2 doubling would change the amount and seasonality of water flow in Canada. The purpose of this paper is then to predict changes in runoff for all of Canada under a proposed $\times 2$ CO_2 atmosphere as predicted by the CCC GCM II (Boer et al. 1992). We then discuss how these changes will vary throughout the country and what are some of the potential implications for ecosystems and water users.

Methods

Data used

Environment Canada has data from extensive climate and hydrology networks that cover much of the northern part of the North American continent. All of the data used in the development of the model were obtained from two Environment Canada databases. Climate data were obtained from the Environment Canada Climate Archive and river discharge data were extracted from Hydat v. 4.94, the Environment Canada Surface Water and Sediment Data CD.

Our site selection was performed by successively filtering each available climate and discharge station through two criteria. First, candidate doublet (climate, hydrology) data sets were to be from sites in as close proximity as possible. For the majority of sites, the weather station was within 10 km of the discharge gauge. For more remote areas, this requirement was relaxed somewhat, but in no case was the weather site further than 60 km from the discharge sites. Second, candidate doublets were required to possess 3 years of monthly summary data for the period 1980–1994 to provide a range of basin conditions that could be used to develop the model.

To match sites from the two databases, a site list with the latitude and longitude for each site was extracted and imported into a common database. A table of candidate sites with coordinates meeting proximity constraints was constructed and each set considered for inclusion. The site selection process yielded 77 suitable sites covering a large extent of Canada (Fig. 1). Each selected basin was examined on topographic maps at a variety of scales to calculate slope for each selected basin. Basin slope served as a crude indicator of the basin's steepness and was calculated as the mean elevation at the upper reaches of the drainage minus the elevation at the water sampling site divided by the distance between the two points (metres per kilometre).

Basins from the Prairies of Canada caused us some particular problems, however. Careful examination of the data showed that there were high numbers of months with very little or no flow in the summer and winter. This was traced to the high incidence of dams, reservoirs, and irrigation structures in this region. As there were great fluctuations in the climate during the same periods, the model obviously could not detect a relationship between precipitation and temperature with runoff and so failed in its predictive capacity. Moreover, these data would not be useful in testing the usefulness of the model. To partially deal with the problem, we acquired flow data from a number of selected basins that were naturalized to take into account water removals by users (J. Chen, Environment Canada, Regina, Sask., personal communication). We did not use these data to develop the model but used them instead to test how well the large-scale models functioned.

Canada is a large country with a wide range of climatic and ecological conditions. Moreover, not all regions of Canada will be affected the same way by global climate changes. In order to provide more useful projections of how runoff might change under a predicted $\times 2$ CO_2 situation, we divided the country into ecologically similar units called "ecozones" (Fig. 1) (Wiken 1986). The largest ecozone is the Boreal Forest, which stretches from Newfoundland to northern Alberta. Because of its large size and because it straddles very different climatic regions, we arbitrarily separated the Boreal Shield into eastern and western components at the Ontario–Manitoba border. Predictions of potential climate change impact on runoff were developed for each river basin selected, and monthly runoff values were averaged for all basins within each ecozone to provide a more easily manageable value.

Specific sites used and their locations and ecozones are identified in the Appendix. The percentage of the ecozones covered by the rivers that we used ranged from 4.3% in the northern southern Arctic/Taiga Shield ecozones to 34% in the Boreal Cordillera (Table 1). Two zones, the Taiga Plains and Montane Cordillera,

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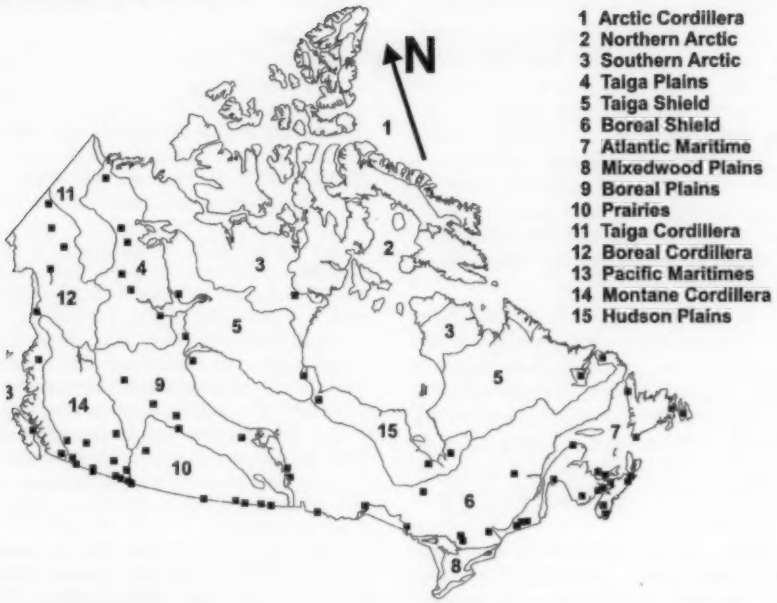
Fig. 1. Location of sampling sites in the ecozones.



showed values greater than 100%, as much of the river basin was outside the ecozone. These data show at least that the data used in the model development were from a substantial portion of each ecozone and not from a minuscule portion of it, which would make the predictions more suspect.

A number of GCMs are available that provide ×2 CO_2 equilibrium climate change scenarios for North America. We selected the CCC GCM II (Boer et al. 1992) seasonal scenarios for temperature and precipitation to provide input data for our model of hydrological changes. We identified the ×2 CO_2 predicted seasonal temperature and precipitation equilibrium values for the area where each individual basin was located. We applied these values (Appendix) to the model for each basin (described below) and calculated new equilibrium monthly runoff. We divided the months into seasons (winter: December–January–February (DJF), spring: March–April–May (MAM), summer: June–July–August (JJA), and autumn: September–October–November (SON)) for easier graphical display.

We realize that large-scale GCM predictions are not ideal for use in fine-resolution problems, especially for precipitation estimates, where regional-scale models are more suitable (Grotch and MacCracken 1991). However, the large-scale models were more easily available and were thus used. As better GCM predictions become available, we will be able to apply them to the hydrological models developed and provide more dependable results.

Model development

A neural network predicting runoff from climatic and geographical inputs was developed using Neuroshell 2 v. 3.0 (Ward Systems Group, Frederick, Md.). Because our data set encompassed basins and runoff values spanning several orders of magnitude, we chose a network architecture designed to make accurate predictions for both midrange and extreme high and low values. This network consisted of the input layer, multiple hidden layers with different activation functions, and an output layer (Fig. 2).

The inputs to the network were the physical parameters of the basin, including basin area, basin slope, latitude and longitude of the discharge gauge, and altitude of the climate station. Climate data for the current and previous months were also presented as inputs and included maximum, minimum, and mean monthly temperature and total monthly rainfall, snowfall, and precipitation. The output predicted by the network was mean monthly runoff (millimetres).

Table 1. Coverage of ecozones by drainage basins in the study and largest individual basin contribution to predictions.

Ecozone	Ecozone coverage (%)	Largest contribution (%)
Atlantic Maritime	5.6	29.4
Boreal Cordillera	34.9	33.7
Boreal Plains	21.7	41.8
Boreal Shield	31.2	50.2
Mixedwood Plains	4.1	85.0
Hudson Plains	3.2	58.9
Taiga Plains	100	82.4
Montane Cordillera	100	40.1
Pacific Maritime	27.6	99.3
Prairies	8.9	62.6
Southern Arctic/Taiga Shield	4.3	81.1
Canada-wide	41.1	18.5

The data set was divided into three disjoint subsets for training the neural network. The majority of cases (80%) were randomly selected for the training set, which was used during the learning process. A test set containing 15% of cases was used to periodically check the progress of learning. The final 5% of cases were reserved in a verification set to check the ability of the trained network to generalize, or produce reasonable predictions for data that it was not trained with.

The actual training process involves initializing the node interconnection weights to some random value. The generated output value for each training set case is then compared with the actual output value and the interconnection weights are adjusted slightly so that the predicted value is somewhat closer to the actual value.

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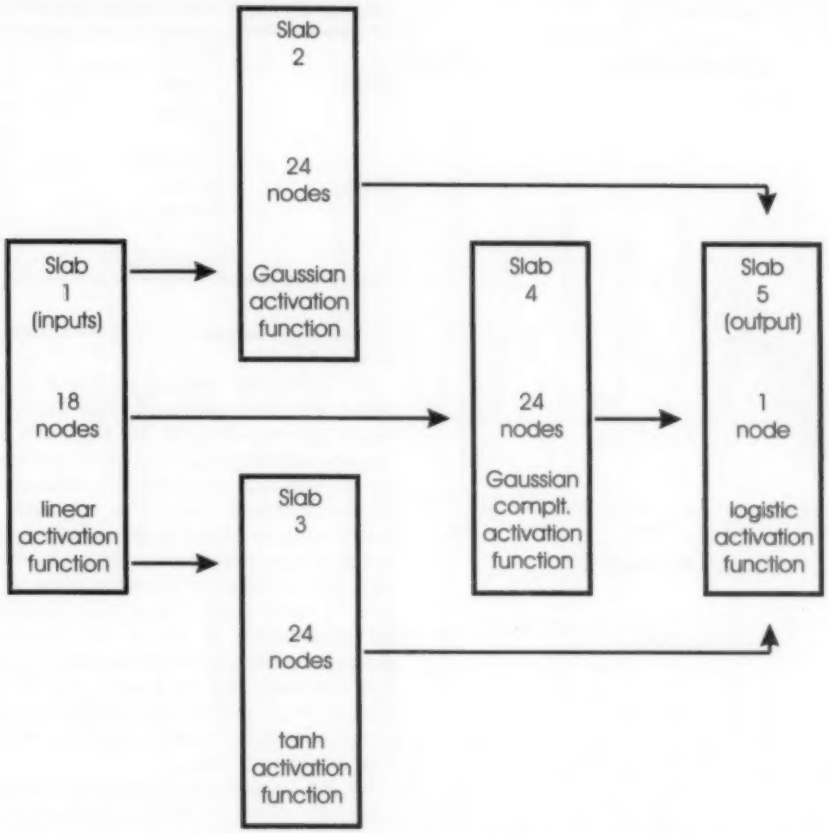
Fig. 2. Neural network design used in the model development.



This process is repeated iteratively until the overall error rate reaches a desired level. Periodically during training, the test set is presented to the network and an overall error prediction is calculated. If the error rate for prediction of the test set is lower than previously calculated, the current state of the network is saved and learning continues. If the error rate of the test set is higher than previous, no changes are made to the saved state. In this way, the learning process is guaranteed to produce a network with the lowest error in prediction and at the same time prevent overlearning or memorization of the test set cases, without the ability to generalize on new data (Rummelhardt and McLelland 1986).

Initially, we subjected all available data to produce one model run. Although overall, the model predicted runoff quite well (R^2 = 0.83) and did well with data for the coastal regions, predictions were very poor for the low-precipitation, low-runoff regions of central and northern Canada. We then split the data into two groups: coastal and temperate areas (Coastal), which include the eastern Boreal Shield, Atlantic Maritime, Pacific Maritime, Mixedwood Plains, Hudson Plains, Montane Cordillera, Taiga and Boreal Cordillera ecozones mostly located in Ontario, Quebec, the Atlantic Provinces, and British Columbia and the central regions (Central), which include southern Arctic, Taiga Shield, Prairies, Taiga Plains, Boreal Plains, and western Boreal Shield. Model predictions for individual ecozones, especially in the Central ecozones, improved considerably under this model reformulation.

The models were run to produce monthly runoff predictions under a $\times 2$ CO_2 atmosphere for each individual river. However, runoff values for all basins in an ecozone were averaged in order to allow for easier regional interpretation.

Results

All available climate and geographical data were introduced into the two artificial neural network (ANN) models developed (Central and Coastal). The estimated runoff was then compared with the measured values to see how well the models could simulate actual conditions (Fig. 3). Overall, both models reproduced actual values well, with the continental margin ecozone model producing a correlation coefficient (R^2) of 0.84 and the Central 0.92. We see that when the predictions were divided among the training, test, and verification sets, the data not used in the model development (the verification set) were not predicted as well as the training and test sets, but nevertheless decreased by only 0.1 in R^2 for the verification set (Table 2).

In order to show concretely how well the model could work, we plotted measured and predicted values for two river basins with long hydrology and climate data sets, the Skeena in the Pacific Maritime (Coastal model site) and Norbert Creek (western Boreal, Central model site) (Fig. 4). We show excellent correlation between both predicted and measured values, even during extreme events. The data we report on are the area-normalized results from 77 sets of individual river basins that were used in model development and prediction under new steady-state climate scenarios.

Summing the absolute values of the interconnection

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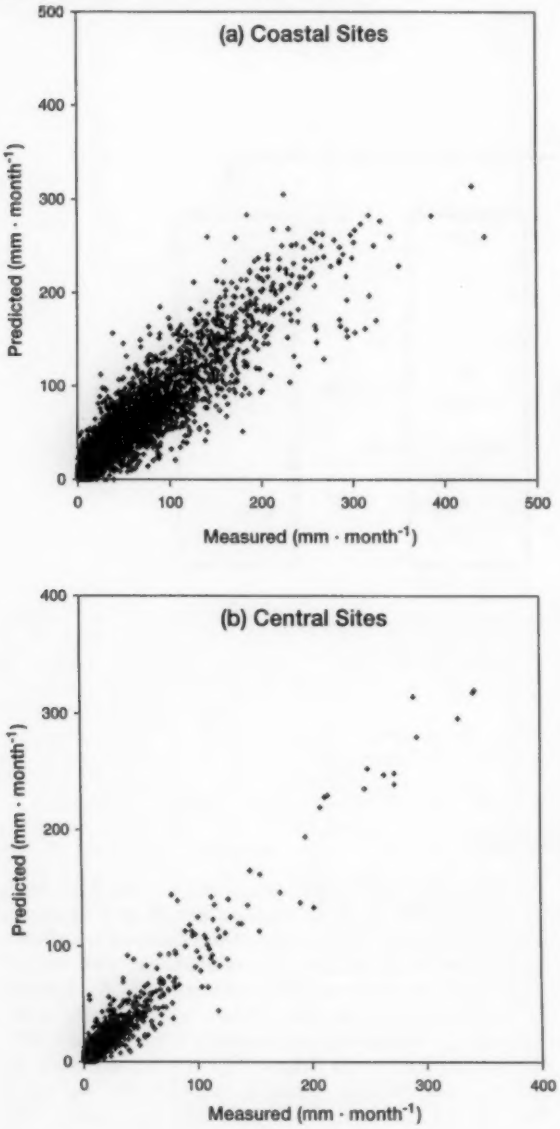
Fig. 3. Comparison of model-predicted and measured runoff values for the Coastal and Central ecozones.



weights for each input node revealed that the most important input contributions to both models come from location on the continent (latitude and longitude), the previous month's maximum temperature, and the month itself (seasonality). The next group in importance was altitude, basin area, and maximum monthly temperature. The greatest difference in contributions between models was in the importance of total rain and basin slopes, both of which were highly important in the Central model. Although they were not identical (nor did we assume that they would be), both models predicted runoff very well when using the available input variables. This gave us the confidence that runoff predictions using ×2 CO_2 scenario temperature and precipitation estimates would be realistic.

Table 2. Correlation coefficients and mean square errors for runoff predictions for the Coastal and Central data sets.

	Data set	R^2	MSE
Coastal	All data	0.84	417.7
	Training	0.85	391.9
	Test	0.81	468.2
	Verification	0.75	674.6
Central	All data	0.93	65.2
	Training	0.94	54.7
	Test	0.84	117.9
	Verification	0.81	67.4

We compared region-normalized cumulative measured values with those predicted under the current conditions for the 12 ecozones (Fig. 5). We show that on an annual basis, our two models predict current annual runoff very well (Table 3), with only one predicted value being worse than 3% off the measured value. This wayward value was for the Prairie ecozone where we did not have good initial data. Our model overpredicted actual measured results by 15.1%. We attempted to improve the predictions by treating this ecozone by itself and by using other manipulation techniques, but were unable to do so. We suggest that the model-generated prediction might represent potential runoff in the Prairie ecozone and have some support in this supposition from Laycock (1987) who showed the difference between precipitation and evapotranspiration in the region to be somewhat less than 50 mm.

We also looked at the cumulative monthly curves to see if seasonally, measured and predicted values varied from each other using a "water year," which we defined as starting from the summer low-flow period. Our results (Fig. 5) show that apart from the Prairie ecozone, there is very good agreement between measured and predicted current conditions throughout the year for all zones.

As our neural network model linking current climate inputs to runoff worked well, we therefore felt that using it to link runoff with the climate values predicted by the CCC GCM II for a ×2 CO_2 scenario was justified. We also decided to modify inputs to the Prairie model for the sake of comparison. Although we realized that the predictions would not be as accurate as those for the other zones, they would at least give us a sense of the direction that runoff would take under a new atmospheric equilibrium.

Increases in total runoff are predicted for the Pacific coast zones. Under the current climatic predictions, we predict that both the Pacific Maritime and Montane Cordillera will show between 12 and 21% increases in runoff annually. As these ecozones already produce over 450 mm in runoff, this is quite significant. We also show that the Boreal Plains will experience a 16% increase, although total amounts will only rise from 123 to 142 mm. However, it may cause significant changes to the flow of large rivers flowing through the region.

The model prediction for the Prairies predicts a 117% increase in runoff, mostly due to increased spring precipitation. As we show above, the model of total runoff for the

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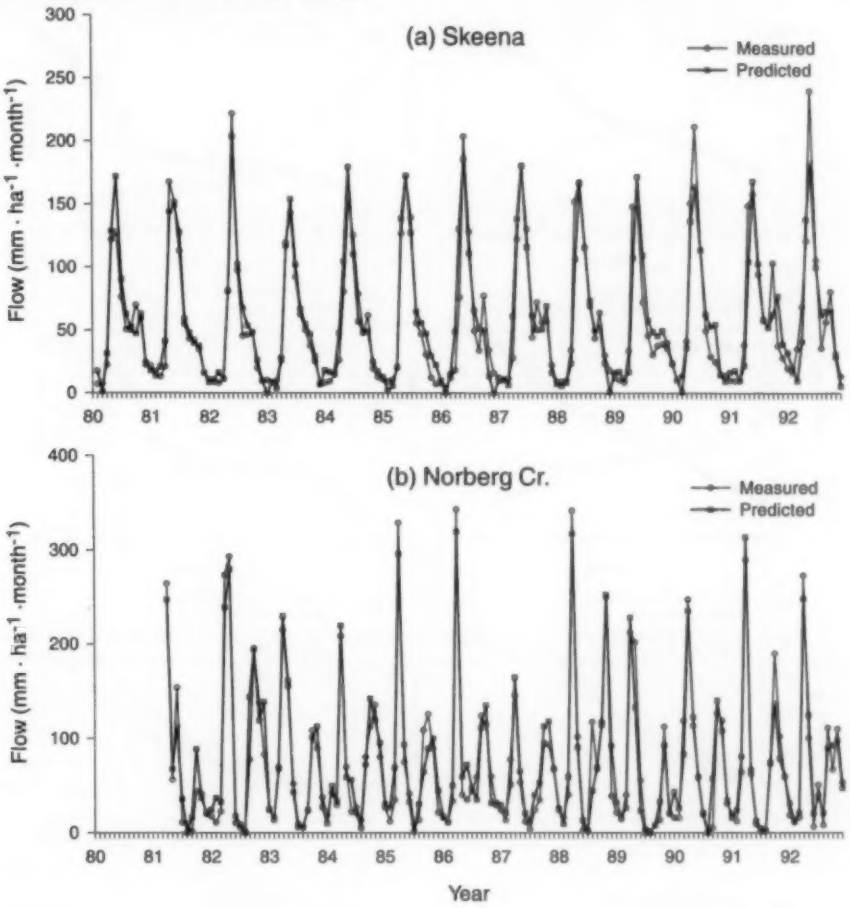
Fig. 4. Measured and predicted monthly runoff values for two of the rivers used in the modeling exercise. The Skeena was done with the Coastal model and Norbert Creek with the Central model.



Prairie ecozone is not as good as for the other zones, but is nevertheless consistent with what happens elsewhere, and the predictions are not too unreasonable.

We show only three of 12 ecozones with reduced annual runoff. The Mixedwood Plains zone is an important contributor to the Great Lakes and St. Lawrence River, as is the eastern Boreal Shield, which we predict will decline slightly. A reduction in water flow to the lakes could lead to serious ramifications for ecosystems and lake water level management regimes. The Hudson Plains zone should also experience a 5.5% runoff decrease, which could have some impact on wetland water levels and thus on the atmospheric fluxes of CO_2 and methane from the large wetland complexes found there.

Although total runoff will not change very much in many ecozones under the new $\times 2$ CO_2 atmospheric equilibrium, how runoff will be distributed throughout the year will change. The model predicts three major types of changes to runoff in most basins (Fig. 6).

Again, the model does not work well for the Prairie ecozone. The model overestimates winter runoff and underestimates spring runoff. We therefore do not have much faith in results from much of the year, even though the prediction of greater spring melting is probably not unreasonable considering the greater spring precipitation predicted by the GCM.

Elsewhere, we predict that winter–spring runoff will be significantly higher than is currently the case in five of the zones (Atlantic Maritime, Boreal Shield (east and west), Boreal Plains, Montane Cordillera). The model also predicts that in most ecozones, maximum and minimum flows will change in timing (Table 4). Spring melt will advance runoff by roughly 1 month in five of the ecozones (Atlantic, Boreal Plains, Montane, Pacific, southern Arctic) and by a few weeks in the others. This will have implications for flood control, irrigation, hydroelectric planning, and a host of ecological effects, such as fish passage and habitat preservation, as well as wetland and lake water levels, which control species diversity and composition.

As interesting as spring melt effects are periods of lowest runoff. There are two patterns of low flow. First, in some southern areas (Atlantic and Mixedwood), lowest flows occur in the summer. Our model predicts that lowest flows in

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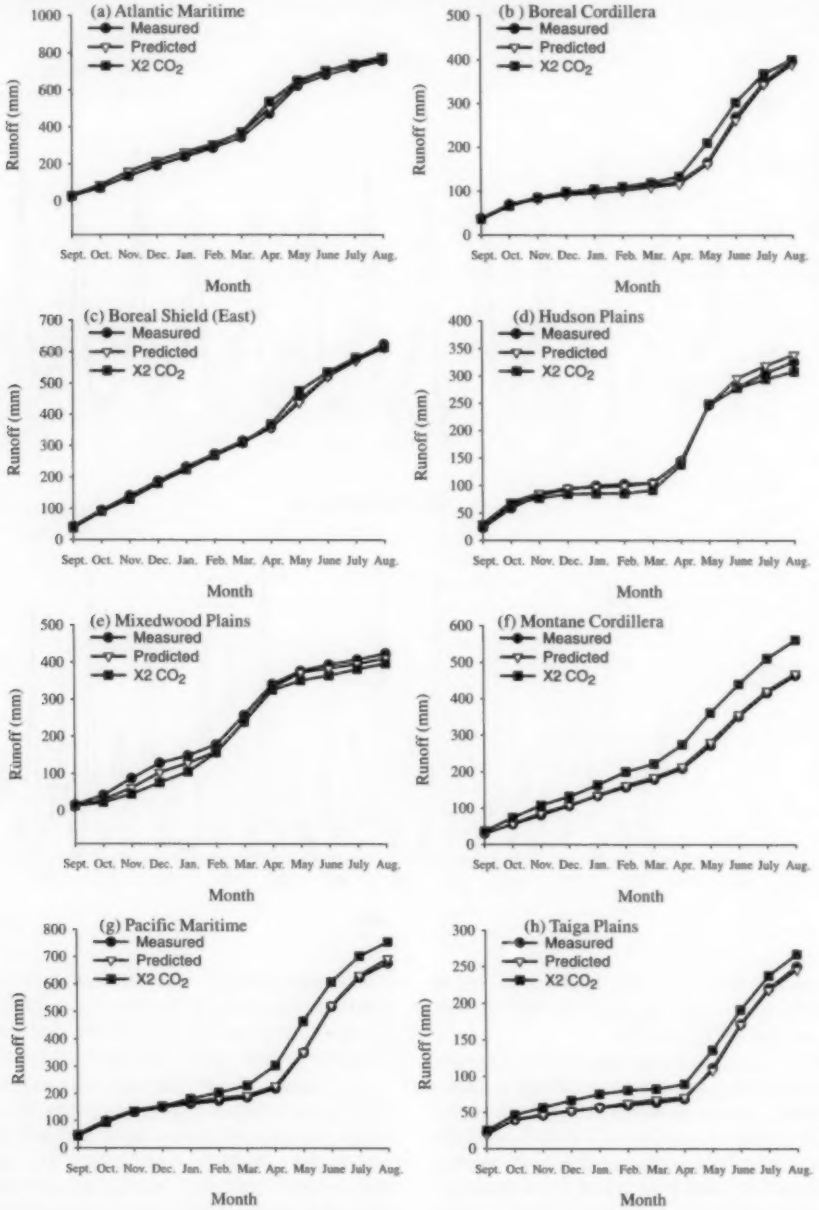
Fig. 5. Averaged measured, predicted current, and ×2 CO_2 cummulative runoff for the ecozones.



the Atlantic will occur earlier than currently (August instead of September), while in the Mixedwood, low flow will change from July to October. Monthly runoff will not change much in either zone, and its significance is difficult to assess.

The most common period for low flows in Canada, however, is during the winter when snowpacks build up and soils are frozen. Our models predict that lowest flow will be earlier than currently by 1 or 2 months for the Boreal Cordillera, Boreal Plains, Hudson Plains, Pacific Maritime, Prairies, and southern Arctic. The low runoff will change from winter to summer in the Boreal Shield (east and west) and will not change in the Taiga and Montane Cordillera.

The change in timing of winter low flows may not be as significant as for high flow, as the runoff amount differences are quite small compared with the spring melts (Fig. 5). However, there are other possible major impacts. For example, nine of the 12 ecozones show lower runoff than currently in the June–August period. This will have an impact on wetland water tables and thus may have a large impact on carbon uptake and release on the large area of wetlands located there (Moore et al. 1998). It should also lower lake

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Fig. 5 (*concluded*).

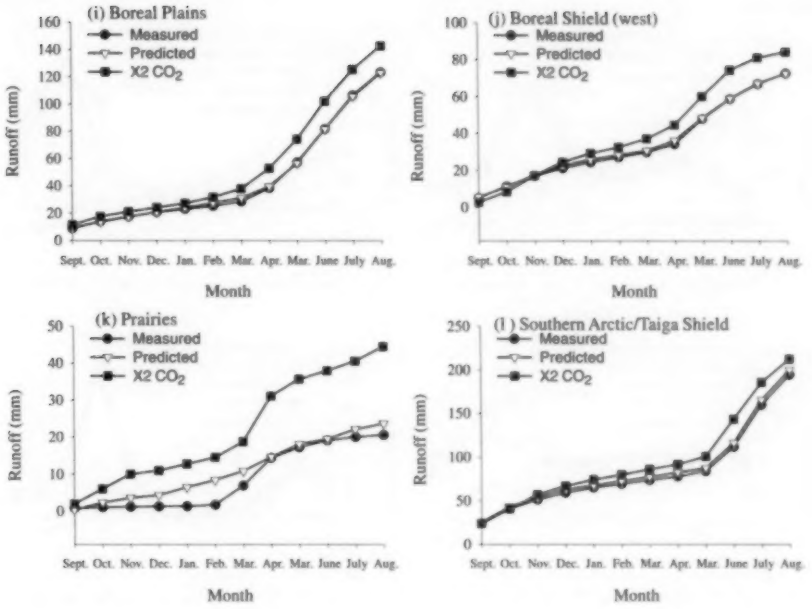

Table 3. Annual runoff measured and predicted actual and potential under an increased CO_2 regime.

Ecozone	Current	Predicted current	% difference	Predicted ×2 CO_2	% change
Atlantic Maritime	756.9	780.2	3.1	766.0	1.20
Boreal Cordillera	397.2	389.8	–1.9	400.3	0.78
Boreal Plains	123.4	122.3	–0.9	142.8	15.72
Boreal Shield (east)	625.3	615.6	–1.6	615.6	–1.55
Boreal Shield (west)	72.9	72.8	–0.1	84.39	15.76
Mixedwood Plains	424.9	411.8	–3.1	398.1	–6.31
Hudson Plains	325.9	339.0	4.0	308	–5.49
Taiga Plains	250.8	246.6	–1.7	267.5	6.66
Montane Cordillera	464.8	469.8	1.1	561.3	20.76
Pacific Maritime	677.7	694.6	2.5	756	11.55
Prairies	20.5	23.6	15.1	44.5	117.07
Southern Arctic/Taiga Shield	194.6	200.4	3.0	212.5	9.20

levels, reduce lake water exchange, and cause warmer water temperatures, which have a number of deleterious ecological consequences (Rouse et al. 1997; Schindler 1997).

Discussion

Our work produces a number of results that we feel are a reasonable first approximation of the changes that should be expected in runoff in Canadian ecozones under a ×2 CO_2 scenario. First, timing of onset and peak runoff will be changed, with earlier starts to spring melts in most regions and earlier peak floods occurring in others. Second, changes in total runoff will occur in many regions where increases in temperature causing increasing evapotranspiration will be more than offset by increases in precipitation. Although the magnitude of the absolute changes may not be well represented by our modeling effort, the direction and trends of the changes are quite likely to be correct. These types of results were also arrived at by Van Barclum et al. (1995), who studied northern river systems. Using a dynamic climate–hydrology model, they predicted a very similar higher and earlier runoff pattern for the Mackenzie and Yukon rivers, confirming our conclusions using a different approach.

As we state above, our predictions for the Prairie ecozone are not as accurate as those for the other ecozones because of the model limitations in dealing with long periods of time with no flow and due to the very high human interference in these rivers. However, the CCC GCM II ×2 CO_2 runs suggest that there will be increases in precipitation in the critical late winter – spring period, which should inevitably lead to greater springtime runoff.

There are a number of other limitations to this work that must be taken into consideration when assessing our model hydrological predictions. First, the number of stations that met our inclusion criteria was relatively low in certain ecozones, so that the information used in the model develop-

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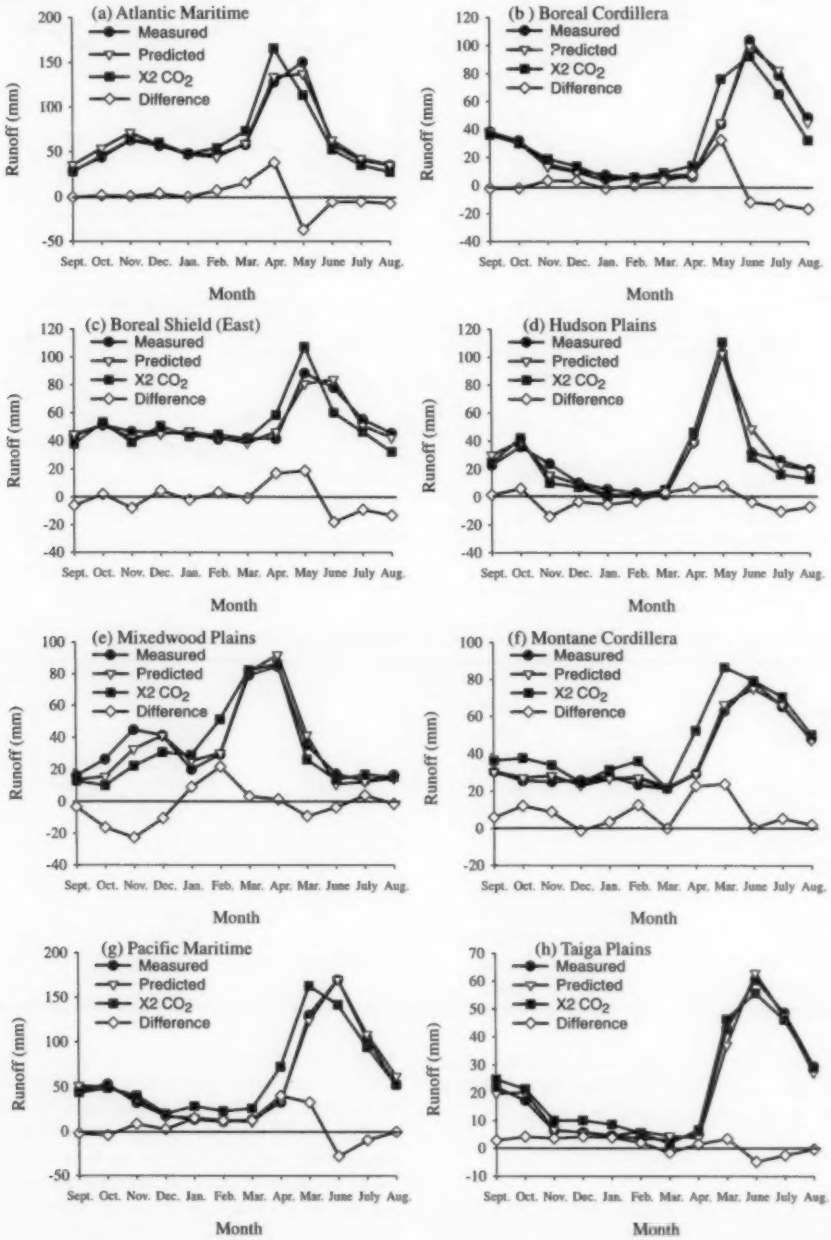
Fig. 6. Averaged monthly measured, predicted current, and ×2 CO_2 runoff. The difference between current and ×2 CO_2 values is displayed on the bottom line.



ment was not as complete as we had hoped for. For example, we only had data for one site on the Taiga Shield and two from the Pacific Maritime zones. Moreover, data series from some of the sites were relatively short. Second, assuming an adequate model linking precipitation and temperature to runoff, we were dependent on temperature and precipitation predictions from GCMs. For example, Slivitsky and Morin (1996) used GCM precipitation and temperature predictions from four different models for the Moisie River in northern Quebec and found differences from current runoff values ranging from −5 to +11.3%. These differences can cause significant variations in runoff predictions when used in empirical models like ours or in deterministic studies. However, GCMs are constantly being refined, and as these improve, temperature and precipitation results can be reintroduced into our hydrological model to produce improved runoff predictions.

The development and use of ANN in predicting hydrolog-

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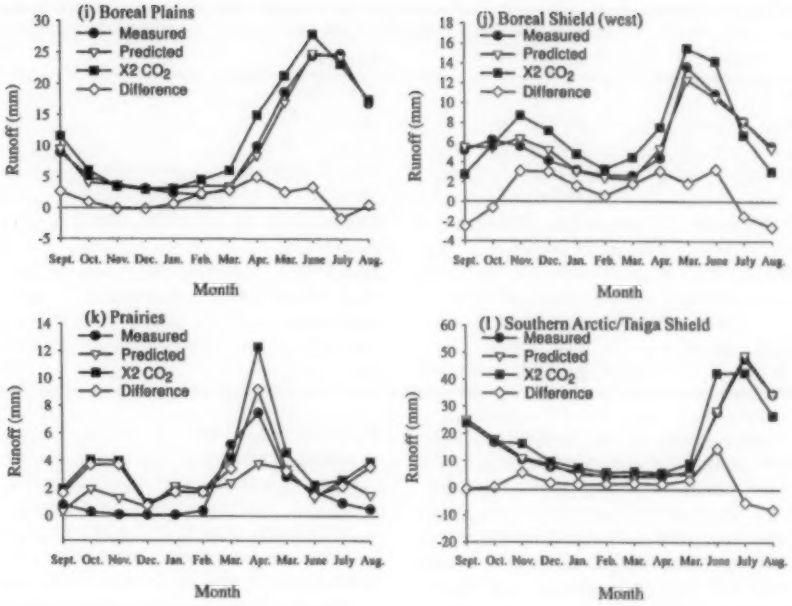
Fig. 6 (*concluded*).



ical phenomena is gaining wide acceptance. Although a number of different approaches within ANN are used in order to optimize the approach (e.g., Hsu et al. 1995; Minns and Hall 1996; Bastarache et al. 1997; Clair and Ehrman 1998), the overall approach is very useful in predicting nonlinear processes using data that are often autocorrelated. These models cannot be used to explain phenomena, but when properly calibrated and evaluated can be very effective predictive tools.

The models take into account a large number of internal basin processes that we cannot directly deal with. For example, in the growing season, runoff in forested and grassland basins is partly controlled by stomatal water conductance of plants (Skiles and Hanson 1994; Aber et al. 1995) and absorption by wetland soils (Boudreau and Rouse 1995; MacLean et al. 1995). These processes, although important in understanding within-basin processes, do not need to be defined individually, as the neural networks look for patterns in the data and not cause–effect relationships.

Repercussions of the changes in runoff that we predict could be important to a number of ecosystem functions and these can be complex and unpredictable (Schindler 1997). Increases in winter and spring runoff amounts will lead to reductions in summer and fall values in many ecozones. Lower summer water levels (Table 4), which will probably be accompanied by higher water temperatures, could have important impacts on fish and other aquatic habitats. For example, based on water warming only, Eaton and Scheller (1996) predicted that up to 50% of coldwater fish habitat could be lost in the United States under a doubling of CO_2. Combining this stress with lower summer runoff could mean serious loss of and changes in fish species from a large number of southern Canadian areas. Moreover, changes in lake stratification and summer and fall depths along with accompanying shifts in algal and zooplankton species distributions and tolerances under lower basin flow conditions could cause shifts in community structure.

Eighteen percent of the Canadian land surface is covered by wetlands (NWWG 1988). As wetlands are defined as areas where the water table is at the soil surface for a considerable period of time, decreases in summer runoff should cause a reduction in wetlands available in the summer for waterfowl nesting and brooding. Sorenson et al. (1998) suggested that breeding duck populations could be reduced by one half in the southern Prairies (U.S. Great Plains) because of the drying up of wetlands in the late spring – early summer period. Our predictions suggest that there should be sufficient water in the Canadian Prairies to ensure that most Canadian sloughs will not be too affected, unlike the situation further south. Moreover, summer decreases in runoff, leading to increasing oxidation of wetland peats, will cause the release of increasing amounts of biogenic CO_2 and methane, which will add to global atmospheric GHG budgets (Gorham 1991).

Lower summer runoff will be counteracted by earlier and higher winter and spring water losses in many regions. This will change flood frequencies and timing. Modifications may be required to floodplain installations, headpond management, and transportation corridors to deal with these changes. On the other hand, our work suggests that summer droughts will be more frequent in some regions, causing changes to municipal, agricultural, and electrical water supplies (Loaiciga et al. 1996). Our work does not specifically address changes in the frequency of extreme flooding or drought events (Caissie and El Jabi 1991), as these are usually caused by extreme climatic events that are not dealt with by GCMs.

Basin-specific studies should be conducted in those regions that we suggest may be most susceptible to large seasonal changes. In particular, human watershed development

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Table 4. Predicted month of peak and minimum runoff under a ×2 CO_2 regime compared with current conditions.

	Maximum runoff month value (mm)		Minimum runoff month value (mm)	
Ecozone	Actual	Predicted	Actual	Predicted
Atlantic Maritime	May (150.4)	Apr. (165.7)	Sept. (28.7)	Aug. (27.5)
Boreal Cordillera	June (104.2)	June (92.5)	Mar. (5.5)	Jan. (5.7)
Boreal Plains	July (24.8)	June (27.9)	Feb. (2.2)	Dec. (3.0)
Boreal Shield (east)	May (88.5)	May (107.5)	Feb. (41.5)	Aug. (32.4)
Boreal Shield (west)	May (13.7)	May (15.6)	Mar. (2.7)	Sept. (2.8)
Hudson Plains	May (102.6)	May (110.9)	Mar. (2.0)	Feb. (0.6)
Mixedwood Plains	Apr. (84.7)	Apr. (86.2)	July (13.1)	Oct. (10.1)
Montane Cordillera	June (79.0)	May (86.7)	Mar. (21.6)	Mar. (21.6)
Pacific Maritime	June (170.1)	May (163.1)	Feb. (10.8)	Dec. (20.0)
Prairies	Apr. (3.1)	Apr. (12.3)	Jan. (0.03)	Dec. (0.9)
Southern Arctic/Taiga Shield	July (47.9)	June (42.6)	Feb. (4.3)	Apr. (5.7)
Taiga Plains	June (60.7)	June (55.9)	Mar. (3.4)	Mar. (1.8)

may be affected by large changes in winter–spring runoff. Design changes to flood control and power-generating structures may have to be undertaken, as well as modifying existing transportation routes. Ecosystem impacts, on the other hand, may be more important with runoff reductions in the summer and fall. Increasing water temperatures due to less water in lakes and rivers and decreased passage and migration opportunities for fish species may cause changes in population structures and distributions.

The types of predictions that we are making could be considered controversial. We believe, however, that the ANN method for linking GCM precipitation and temperature data is sound and that as better regional climate models are developed, we can use them to improve our runoff predictions. As better regional climate change models are developed and a better understanding of how to deal with the Prairie data is arrived at, we will be in a position to improve our predictions and get a better assessment of the true impact of climate change on Canadian ecosystems.

Acknowledgments

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References

Aber, J.D., Olliger, S.V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W., Melillo, D.J., and Lathrop, R.G., Jr. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. Clim. Res. **5**: 207–222.

Bastarache, D., El-Jabi, N., Turkhan, N., and Clair, T.A. 1997. Predicting conductivity and acidity for two small streams using learning networks. Can. J. Civ. Eng. **24**: 1030–1039.

Boer, G.J., McFarlane, N.A., and Lazare, M. 1992. Greenhouse gas-induced climate change simulated with the CCC second-generation general circulation model. J. Clim. **5**: 1045–1077.

Boudreau, L.D., and Rouse, W.L. 1995. The role of individual terrain units in the water balance of wetland tundra. Clim. Res. **5**: 31–47.

Caissie, D., and El-Jabi, N. 1991. A stochastic study of floods in Canada: frequency analysis and regionalization. Can. J. Civ. Eng. **18**: 225–236.

Clair, T.A., and Ehrman, J.M. 1996. Variation in discharge, dissolved organic carbon and nitrogen export from terrestrial basins with changes in climate: a neural network approach. Limnol. Oceanogr. **41**: 921–927.

Clair, T.A., and Ehrman, J.M. 1998. Using neural networks to assess the influence of changing seasonal climates in modifying discharge, dissolved organic carbon and nitrogen export in eastern Canadian rivers. Water Resour. Res. **34**: 447–455.

Eaton, J.G., and Scheller, R.M. 1996. Effects of climate warming on fish thermal habitat instreams of the United States. Limnol. Oceanogr. **41**: 1109–1115.

Frederick, K.D., and Major, D.C. 1997. Climate change and water resources. Clim. Change, **37**: 7–23.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. **1**: 182–195.

Grotch, S.L., and MacCracken, M.C. 1991. The use of General Circulation Models to predict regional climate change. J. Clim. **4**: 286–303.

Hsu, K.-L., Gupta, H.V., and Sorooshian, S. 1995. Artificial neural network modeling of the rainfall–runoff process. Water Resour. Res. **31**: 2517–2530.

Laycock, A.H. 1987. The amount of Canadian water and its distribution. Chap. 2. *Edited by* M.C. Healy and R.R. Wallace. Can. Bull. Fish. Aquat. Sci. No. 215. pp. 13–42.

Loaiciga, H.A., Valdes, J.B., Vogel, R., Garvey, J., and Schwarz, H. 1996. Global warming and the hydrologic cycle. J. Hydrol. **174**: 83–127.

MacLean, R.A., English, M.C., and Schiff, S.L. 1995. Hydrological and hydrochemical response of a small Canadian Shield catchment to late winter rain-on-snow events. Hydrol. Processes, **9**: 845–863.

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Manabe, S., Stouffer, R.J., Spelman, M.J., and Bryan, K. 1991. Transient responses of a coupled ocean–atmosphere model to gradual changes in atmospheric CO_2. Part II. Seasonal response. J. Clim. **4**: 105–126.

Minns, A.W., and Hall, M.J. 1996. Artificial neural networks as rainfall–runoff models. Hydrol. Sci. J. **41**: 399–417.

Moore, T.M., Roulet, N.T., and Waddington, J.M. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. Clim. Change. **40**: 229–245.

National Wetlands Working Group (NWWG). 1988. Wetlands of Canada. Ecological Land Classification Series 24. Environment Canada, Ottawa, Ont.

Rouse, W.R., Douglas, M.S.V., Hecky, R.E., Hershey, A.E., Kling, G.W., Lesack, L., Marsh, P., McDonald, M., Nicholson, B.J., Roulet, N.T., and Smol, J.P. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. Hydrol. Processes, **11**: 873–902.

Rumelhardt, D.E., and McClelland, J.L. 1986. Parallel distributed processing: explorations in the microstructure of cognition. MIT Press, Cambridge, Mass.

Russell, G.L., Miller, J.R., and Rind, D. 1995. A coupled atmosphere–ocean model for transient climate change studies. Atmos.-Ocean, **33**: 683–730.

Schindler, D.W. 1997. Widespread effects of climate warming on freshwater ecosystems in North America. Hydrol. Processes, **11**: 1042–1067.

Schindler, D.W., Curtis, P.J., Parker, B.R., and Stainton, M.P. 1996. Consequences of climate warming and lake acidification for UV-B penetration in North American lakes. Nature (Lond.), **379**: 705–707.

Skiles, J.W., and Hanson, J.D. 1994. Responses of arid and semi-arid watersheds to increasing carbon dioxide and climate change as shown by simulation studies. Clim. Change, **26**: 377–397.

Slivitsky, M., and Morin, G. 1996. Impacts of climatic changes on the hydrological regime: the Moisie River case revisited. Bull. Can. Meteorol. Ocean. Soc. 24-4.

Sorenson, L.G., Goldberg, R., Root, T.L., and Anderson, M.G. 1998. Potential effects of global warming on waterfowl populations breeding in the northern Great Plains. Clim. Change. **40**: 343–369.

Stemberger, R.S., Hierlihy, A.T., Kugler, D.L., and Paulsen, S.G. 1996. Climatic forcing on zooplankton richness in lakes of the northeastern United States. Limnol. Oceanogr. **41**: 1093–1101.

Van Barclum, S.C., Miller, J.R., and Russel, G.L. 1995. High latitude river runoff in a doubled CO_2 climate. Clim. Change, **30**: 7–26.

Wiken, E.B. 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series No. 19. Environment Canada, Hull, Que.

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Appendix. River name, Hydat No., and gauge location used in the model and temperature and precipitation changes for each season at each site.

Station	Name	Ecozone	Latitude	Longitude	CCC GCM II mean seasonal temperature change (°C)				CCC GCM II mean seasonal precipitation change (%)			
					DJF	MAM	JJA	SON	DJF	MAM	JJA	SON
01AD001	MADAWASKA	Atlantic Maritime	47.54	–68.63	5	3	4	2	10	0	–10	–10
02QC001	MADELEINE	Atlantic Maritime	49.2	–65.29	6	3	3	2	0	0	–10	–10
01AM001	NW OROMOCTO	Atlantic Maritime	45.67	–66.68	4	3	4	3	10	0	–10	–10
01BV006	PT. WOLFE	Atlantic Maritime	45.55	–65.01	4	3	3	3	10	0	–10	–10
01CA003	MILL	Atlantic Maritime	46.74	–64.18	5	4	3	3	0	0	–10	–10
01CB002	DUNK	Atlantic Maritime	46.34	–63.63	5	4	3	3	0	0	–10	–10
01DL001	KELLY	Atlantic Maritime	45.58	–64.45	4	3	3	3	10	0	–10	–10
01DN004	WALLACE	Atlantic Maritime	45.67	–63.55	4	4	3	3	0	0	–20	–10
01EC001	ROSEWAY	Atlantic Maritime	43.83	–65.37	3	3	3	3	10	0	–20	–10
01ED007	MERSEY	Atlantic Maritime	44.43	–65.22	4	3	3	3	10	0	–10	–10
01EO001	ST. MARYS	Atlantic Maritime	45.17	–61.98	4	3	3	3	0	0	–20	–10
01ER001	CLAM HARBOUR	Atlantic Maritime	45.46	–61.46	4	3	3	3	0	0	–20	–10
02YC001	TORRENT	Atlantic Maritime	50.6	–57.15	6	4	3	2	0	0	0	10
02ZB001	ISLE AUX MORTS	Atlantic Maritime	47.61	–59	4	4	3	3	0	–10	–10	0
02ZH001	PIPERS HOLE	Atlantic Maritime	47.94	–54.28	4	4	3	3	10	0	0	0
02ZK001	ROCKY	Atlantic Maritime	47.22	–53.56	4	4	3	3	10	0	0	0
08CF001	STIKINE	Boreal Cordillera	57.48	–131.75	4	5	4	3	10	0	10	10
09AE001	TESLIN	Boreal Cordillera	60.48	–133.3	4	4	4	3	10	0	10	20
09BC001	PELLY	Boreal Cordillera	62.82	–136.58	3	3	5	4	0	10	20	10
09BC004	PELLY	Boreal Cordillera	62.22	–133.37	4	3	4	3	10	0	10	20
09EA003	KLONDIKE	Boreal Cordillera	64.04	–139.4	2	4	5	4	0	10	20	10
05EF001	N.SASKATCHEWAN	Boreal Plains	53.51	–109.61	7	5	3	2	30	30	0	20
05KH007	CARROT	Boreal Plains	53.6	–102.11	6	4	4	3	20	20	–20	10
06AD006	BEAVER	Boreal Plains	54.35	–110.21	7	5	3	2	30	20	0	20
07BE001	ATHABASCA	Boreal Plains	54.72	–113.28	6	4	3	2	20	20	–10	30
07GJ001	SMOKY RIVER	Boreal Plains	55.71	–117.62	5	3	3	2	10	10	–10	20
07NB008	DOG	Boreal Plains	59.87	–111.52	6	3	3	2	0	0	–10	20
02AC002	BLACK STURGEON	Boreal Shield	48.9	–88.37	6	3	4	3	10	20	–10	10
02BF009	NORBERG CREEK	Boreal Shield	47.06	–84.4	6	4	4	3	0	20	0	–10
02EA010	AGNETAWAN	Boreal Shield	45.7	–79.3	6	5	4	3	0	10	0	–20
02KC009	BONNECHERE	Boreal Shield	45.49	–76.56	5	4	4	3	0	0	0	–20
02RD002	MISTASSIBI	Boreal Shield	48.89	–72.21	5	3	4	2	10	10	–10	–10
03OE001	CHURCHILL(Labrador)	Boreal Shield	53.24	–60.78	7	4	4	2	0	10	–10	0
03QC001	EAGLE	Boreal Shield	53.53	–57.49	6	4	2	1	0	10	0	0
04AB001	HAYES	Boreal Shield	56.43	–92.78	8	3	4	2	20	10	0	10
04LD001	GROUNDHOG	Boreal Shield	49.36	–82.04	5	3	4	3	–10	20	0	–10
05PC019	RAINY	Boreal Shield	48.6	–93.4	6	4	4	3	20	10	–20	10
05RA001	MANIGOTAGAN	Boreal Shield	51.09	–96.28	7	5	4	3	10	10	–20	20
05RB003	BLOODVEIN	Boreal Shield	51.71	–96.61	7	4	5	3	10	10	–20	20
06FD001	CHURCHILL	Boreal Shield	58.12	–94.62	7	3	5	3	20	10	0	20
07MA003	DOUGLAS	Boreal Shield	58.32	–109.78	6	2	3	2	0	0	0	20

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Appendix (*concluded*).

Station	Name	Ecozone	Latitude	Longitude	CCC GCM II mean seasonal temperature change (°C)				CCC GCM II mean seasonal precipitation change (%)			
					DJF	MAM	JJA	SON	DJF	MAM	JJA	SON
06DE008	TURKEY STREAM	Boreal Shield	45.33	–79.21	6	5	4	3	0	0	0	–30
02OA054	CHATEAUGUAY	Mixedwood Plains	45.33	–73.76	5	4	4	3	0	0	0	–10
02OG007	YAMASKA NORD	Mixedwood Plains	45.41	–72.62	5	4	4	3	0	0	0	–10
02OJ024	HURONS	Mixedwood Plains	45.49	–73.18	5	4	4	3	0	0	0	–10
05AA023	OLDMAN RIVER	Montane Cordillera	49.81	–114.18	5	5	3	2	30	20	–10	10
05AE027	ST. MARY RIVER	Montane Cordillera	49	–113.31	6	5	3	3	30	20	–10	0
05DA009	.N. SASK.	Montane Cordillera	52	–116.46	5	4	3	2	20	10	–10	20
08LE021	SALMON	Montane Cordillera	50.69	–119.37	4	4	3	2	20	0	–10	20
08LF051	THOMPSON	Montane Cordillera	50.35	–121.39	4	4	2	3	20	–10	–20	20
08MF005	FRASER AT HOPE	Montane Cordillera	49.38	–121.45	4	4	2	3	20	–10	–20	10
08NE049	COLUMBIA	Montane Cordillera	49.17	–117.71	4	4	3	3	20	0	–10	10
08NE058	COLUMBIA	Montane Cordillera	49	–117.62	4	4	3	3	20	0	–10	10
08NF002	KOOTENAY	Montane Cordillera	50.14	–115.79	5	4	3	2	20	10	–10	10
08NK005	ELK RIVER	Montane Cordillera	49.21	–115.11	5	5	3	3	20	10	–10	10
08NL038	SIMILKAMEEN	Montane Cordillera	49.37	–120.15	4	4	3	3	20	–10	–20	10
08NM085	OKANAGAN	Montane Cordillera	49.11	–119.56	4	4	3	3	20	–10	–10	10
08NP003	HOWELL CREEK	Montane Cordillera	49.09	–114.53	5	5	3	3	20	10	–10	0
08EF001	SKEENA	Pacific Maritime	54.63	–128.43	3	4	3	3	10	0	0	10
08HD005	QUINSAM	Pacific Maritime	50.02	–125.29	3	3	3	3	30	–10	–20	10
05AD005	BELLY	Prairies	49.1	–113.69	6	5	3	3	30	20	–10	0
05CE001	RED DEER	Prairies	51.46	–112.71	6	6	3	2	30	30	–10	10
05ND001	SOURIS	Prairies	49.18	–102.02	7	8	5	3	–20	40	–20	0
05NF002	ANTLER	Prairies	49.05	–101.04	7	8	5	3	–20	40	–20	0
05OA007	BADGER CREEK	Prairies	49.1	–99.32	7	8	5	3	–20	30	–20	10
05OB007	PEMBINA	Prairies	49.03	–98.27	7	8	4	3	–10	30	–20	20
11AE003	EAST POPLAR	Prairies	48.99	–105.4	7	9	4	3	0	50	–20	–10
06LC001	KAZAN	Southern Arctic	63.65	–95.85	5	3	5	4	0	0	10	20
07OB001	HAY	Taiga Plains	60.74	–115.86	5	3	3	3	–5	0	–10	20
10ED002	LIARD	Taiga Plains	61.74	–121.22	5	3	3	3	0	0	10	10
10GA001	ROOT	Taiga Plains	62.48	–123.43	5	3	3	3	10	0	10	10
10HC003	BIG SMITH CREEK	Taiga Plains	64.59	–124.81	5	3	3	4	0	–10	0	10
10KA001	MACKENZIE	Taiga Plains	65.27	–126.84	4	3	3	4	0	–10	0	10
10LC003	RENGLENG	Taiga Plains	67.75	–133.85	4	5	4	4	0	20	10	0
07SB002	YELLOWNKIFE	Taiga Shield	62.54	–114.16	5	3	3	3	30	0	–10	20
03BF001	PONTAX	Hudson Plains	51.53	–78.10	6	3	4	2	10	10	–10	10
04KA001	KWATABOAHEGAN	Hudson Plains	51.15	–80.87	6	3	4	3	–10	20	10	10

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Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes

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Abstract: In an alpine area of the Sierra Nevada of California, naturally acidic waters and introduced fishes both strongly affect the distributions of native amphibians, zooplankton, and macroinvertebrates. The study area in Kings Canyon National Park contains 104 lakes with pH values between 5.0 and 9.3, including 10 lakes with pH < 6.0 (defined here as acidic lakes) and 18 lakes with introduced trout. We surveyed 33 of these lakes (8 acidic, 7 non-acidic with trout, 18 non-acidic without trout) for water chemistry and faunal assemblages. Yellow-legged frog tadpoles (*Rana muscosa*), common microcrustaceans (*Daphnia, Hesperodiaptomus, Diaptomus*), and larvae of a caddisfly (*Hesperophylax*) were rare or absent in acidic lakes but common in non-acidic lakes, and microcrustacean and macroinvertebrate species richness decreased with decreasing pH. Large and (or) mobile, conspicuous taxa, including tadpoles, large-bodied microcrustaceans (*Hesperodiaptomus, Daphnia middendorffiana*), and many epibenthic or limnetic macroinvertebrates (baetid and siphlonurid mayfly nymphs, notonectids, corixids, limnephilid caddis larvae, and dytiscid beetles), were rare or absent in trout lakes but were relatively common in lakes lacking trout, and the taxon richness of macroinvertebrates was reduced by trout.

Résumé : Dans un secteur alpin de la chaîne de la Sierra Nevada, en Californie, les eaux acides naturelles et les poissons introduits exercent une profonde influence sur la répartition des espèces indigènes d'amphibiens, de zooplancton et de macroinvertébrés. La zone d'étude, située dans le parc national Kings Canyon, renferme 104 lacs dont le pH varie entre 5,0 et 9,3, y compris 10 lacs présentant un pH < 6,0 (définis ici comme des lacs acides) et 18 lacs contenant des truites introduites. Nous avons étudié la chimie de l'eau et la composition faunistique de 33 de ces lacs (8 lacs acides, 7 lacs non acides contenants des truites et 18 lacs non acides sans truites). Des têtards de la grenouille *Rana muscosa*, des microcrustacés communs (*Daphnia, Hesperodiaptomus, Diaptomus*) et des larves d'un éphéméroptère (*Hesperophylax*) étaient rares ou absents dans les lacs acides, mais communs dans les lacs non acides, et le nombre d'espèces de microcrustacés et de macroinvertébrés diminuait en fonction de l'acidité. Les taxons de plus grande taille et(ou) mobiles et plus visibles comme les têtards, les gros microcrustacés (*Hesperodiaptomus, Daphnia middendorffiana*) et de nombreux macroinvertébrés épibenthiques ou limnétiques [larves de baetides et de siphlonurides (éphéméroptères), notonectides, corixides, larves de limnéphilides (Trichoptères) et dystiscides] étaient rares ou absents dans les lacs contenant des truites, mais relativement communs dans les lacs sans truites. Le nombre de taxons de macroinvertébrés était moins élevé dans les lacs contenant des truites.

[Traduit par la Rédaction]

Introduction

It is well known that abiotic factors, such as water chemistry, and biological interactions, such as predation, can affect the diversity, biomass, and species composition of freshwater animal communities (Brett 1989; Magnuson et al. 1984; Locke 1992; Brezonik et al. 1993). For example, the effects of fish on freshwater zooplankton communities are strong and well documented (Brooks and Dodson 1965; Anderson 1980). Moreover, chemical characteristics of lakes, such as acidity, impose constraints on the distribution of freshwater organisms with repercussions for the structure of the community and the intensity of biological interactions (Freda 1990; Havens 1993; Locke 1992). There have been few studies, however, on the effects of acidity and trophic structure on lake communities in the western U.S.

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(Stoddard 1987; Barmuta et al. 1990; Bradford et al. 1993, 1994*b*).

Although almost all lakes at high elevations in the Sierra Nevada (i.e., >2600 m elevation, defined herein as "High Sierra") have a pH > 6, a small number of acidic lakes (pH < 6) were recently discovered in the Mt. Pinchot area of Kings Canyon National Park, California, U.S.A. (Whiting et al. 1989; Bradford et al. 1994*a*). The source of acidity in this area is sulfuric acid produced by the oxidation of pyrite found in metamorphic and granitic rocks (Mahood and Gansecki 1993; Bradford et al. 1994*a*). Unlike typical Ca^{2+}–Na^{+}–HCO_3^{-}-dominated Sierran lakes, SO_4^{-2} is the dominant anion in 19 of the lakes in this area, including all of the acidic lakes (Melack and Stoddard 1991; Bradford et al. 1994*a*). The mixture of acidic and non-acidic lakes found in this area allowed us to evaluate relationships between long-term, acidic conditions and the distribution of the aquatic biota. Because most of the lakes in the High Sierra are very dilute and weakly buffered, there is concern that future increases in acid loading from anthropogenic sources could result in acidification of these lakes with attendant decreases in aquatic biodiversity (Melack et al. 1989; Barmuta et al. 1990; Melack and Stoddard 1991; Bradford et al. 1994*b*). The characteristics of naturally acidic lakes, then, may provide an indication of the long-term effects of potential cultural acidification on the composition of lake communities in the High Sierra.

Furthermore, many of these lakes have not been stocked with fish because of their remote locations, allowing us to evaluate the effects of trophic structure (presence vs. absence of fish) on lake communities. Nearly all of the montane lakes and streams in western North America were originally devoid of fish (Bahls 1992). In the last century, however, many of these waters were stocked with fish, particularly trout, to provide recreational fisheries. It has been estimated that approximately 60% of the montane lakes in western North America now contain fish, including 95% of the larger (>2 ha) and deeper (>1.5 m) lakes (Bahls 1992). The effects of non-native fish introductions on the native biota have been little studied in High Sierra waters; however, limited observations suggest that introduced fish have caused declines in native aquatic invertebrates and amphibians (Melack et al. 1989; Stoddard 1987; Bradford et al. 1993). Because most High Sierra waters now contain introduced trout, the effects of these introductions on biodiversity may be substantial (Knapp 1996).

The goal of this study was to examine relationships among lake acidity (e.g., pH), other water chemical parameters (e.g., major ion concentrations), the presence of non-native fish, and zooplankton, macroinvertebrate, and amphibian assemblages (e.g., taxon presence–absence, abundance, and (or) taxon richness). We hypothesized that large, conspicuous, exposed taxa would be reduced or eliminated where fish predators are present (Brooks and Dodson 1965; Northcote 1988) and that taxa shown to be especially sensitive to acidic conditions would be rare or absent in acidic lakes (Brett 1989; Melack et al. 1989). We surveyed chemical conditions and the presence–absence of vertebrate populations in 104 lakes in the Mt. Pinchot area and then chose a subset of 33 of these lakes for detailed analyses of water chemistry, fish, amphibians, zooplankton, and macroinvertebrates. We compared our survey results with the results of earlier short-term, small-scale field experiments and laboratory studies in which acidity was manipulated to examine congruence between these observational and experimental approaches.

Materials and methods

Study area and design of study

The study area was approximately 50 km^2 in area, located in Kings Canyon National Park in eastern California (Fig. 1). This area includes 11 catchments, six that drain into the South Fork of the Kings River and five that drain into Woods Creek (Fig. 1). The geological formations of the study area are a complex mixture of large granodiorite masses and metasedimentary roof pendants, including biotite schist, calc-hornfels, marble, and peltic hornfels and quartzite (Moore 1963). The study area encompassed four Sierra Nevada lakes recently found to have pH values of 4.6 to 5.2 (Whiting et al. 1989; Bradford et al. 1994*b*; Jenkins et al. 1994). These are lower than the lowest summer pH reported for other lakes in the Sierra Nevada (pH 5.6) and are also lower than pH values reported for all but one of the lakes surveyed in the western U.S. by the Environmental Protection Agency's Western Lake Survey (Melack et al. 1985; Landers et al. 1987; Melack et al. 1989; Whiting et al. 1989; Jenkins et al. 1994; Stoddard 1995).

The study consisted of a synoptic survey and a detailed survey. In the synoptic survey, we documented chemical conditions and the presence–absence of vertebrate populations in 104 high-elevation lakes (>3100 m elevation), representing all lakes in the study area (Fig. 1). For the detailed survey, 33 lakes were chosen from the above set for detailed analyses of their chemical and biological characteristics. We first chose all of the acidic lakes (pH < 6) in this area because of their rarity, except for two that were extremely shallow (<0.5 m depth) and near larger, deeper acidic lakes. Second, we chose two lakes (Bench and Marjorie), both containing fish, because chemical data had been collected from them in previous studies. We chose five additional fish lakes near acidic lakes, attempting to match the elevation, size, and depth of these lakes to the acidic lakes. These attempts to match the physical characteristics of fish and acidic lakes were only partially successful because fish tended to occupy the largest and deepest lakes in this area. Finally, we chose 18 non-acidic (pH > 6) fishless lakes near acidic and fish lakes so that their elevations, sizes, and depths matched those of acidic lakes (pH < 6.0) as closely as possible. We chose pH 6.0 as the cut-off for delineating acidic vs. non-acidic lakes because previous experimental studies indicated that sensitive taxa begin to decline between pH 5.5 and 6 (Melack et al. 1989; Barmuta et al. 1990). Because fish were absent in acidic lakes, these procedures provided 8 acidic lakes, 7 fish lakes, and 18 non-acidic, fishless lakes for comparisons.

Synoptic survey

The 104 lakes in the synoptic survey were surveyed between 29 June and 4 July, 1992, for the presence–absence of fish and amphibians by walking along the shoreline of most or all of each lake (Bradford et al. 1994*b*). Because these lakes were extremely clear and often small, large areas of these lakes could be viewed from shore. Later, gill net surveys (see Detailed survey section) showed that shoreline surveys accurately assessed the presence or absence of fish. Amphibians were captured by hand net if necessary to identify species. Amphibians were recorded as either tadpoles or "adults" (defined as metamorphosed individuals, regardless of size). pH and specific conductance were measured in the field on the same day as sampling using standard methods (described below). Elevation and lake area were determined from topographic maps. Maximum lake depth was estimated visually to 0.5 m up to

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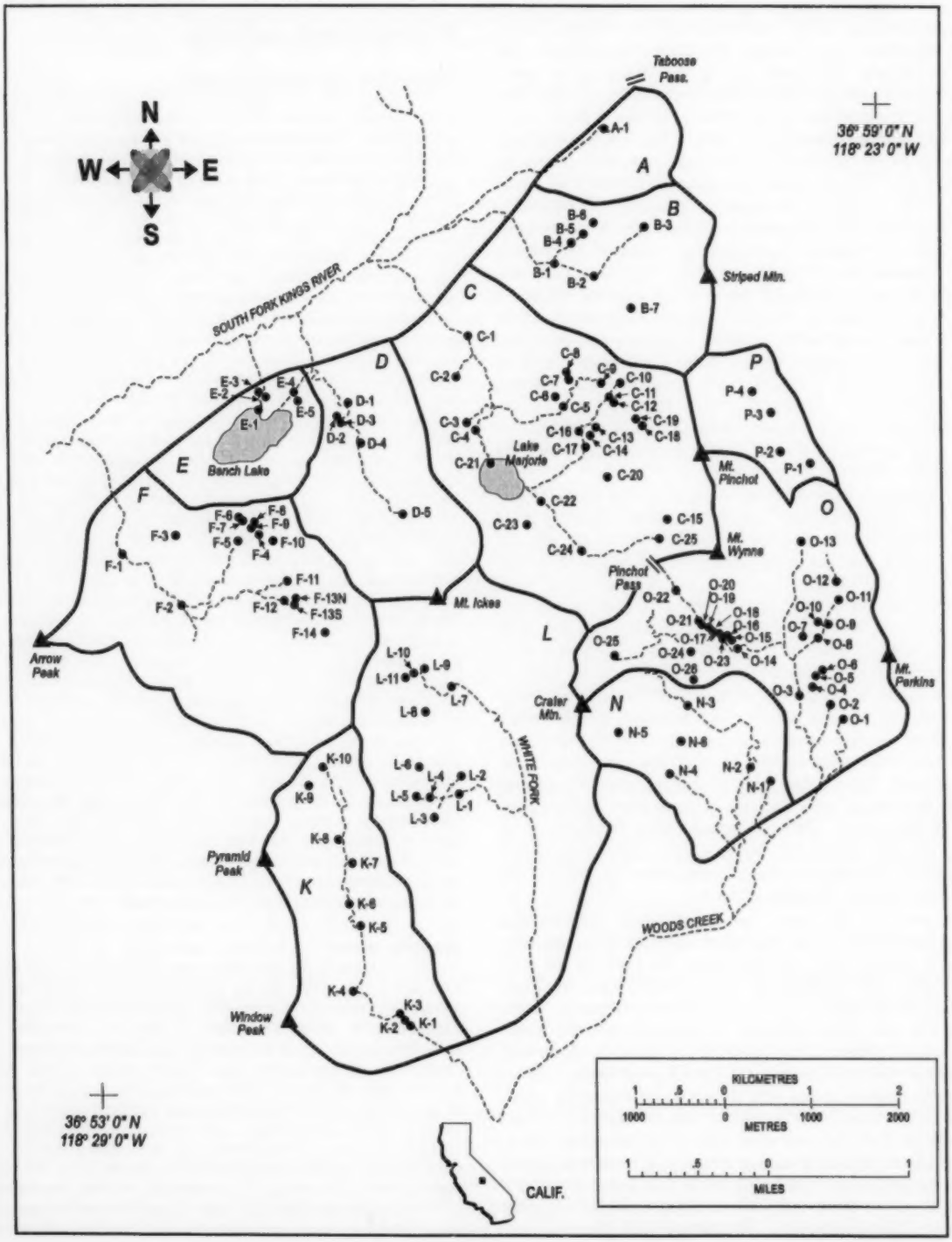
Fig. 1. Study area showing catchment boundaries, Kings Canyon National Park, California. Closed, labeled circles correspond to lakes shown on base map (U.S. Geological Survey, 7 1/2′ quadrangle, Mt. Pinchot, Calif., Provisional Edition, 1985). The 33 lakes in the detailed survey are as follows: acidic lakes (C-22, -24; F-1, -2, -13N, -14; L-7, -11), fish lakes (B-1; C-4, -5, -21; D-4; E-1; N-3), and non-acidic, fishless lakes (B-5; C-2, -10, -17, -23; D-5; E-4; F-4, -11, -12, -13S; L-1, -8, -9; O-7, -8, -21; P-3). Inset map shows location of this area in California.



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a maximum of 5 m. Subsequent measurements of 32 lakes by plumb line in the detailed survey were highly correlated with these estimated values (Spearman rank correlation test, $p < 0.001$).

Detailed survey

For the 33 lakes chosen, we collected samples of fish, macroinvertebrates, zooplankton, and water and recorded observations of amphibians between 11 August and 1 September 1992. Fourteen of the 33 lakes were sufficiently shallow and clear that investigators could scan the whole water mass from the shoreline or a small raft to ascertain the presence or absence of fish. Fish populations were surveyed in the remaining 19 lakes by using a gill net, which was 43.5 m long, 1.5 m deep, and consisted of 6 equal-sized panels with mesh sizes of 2.5, 3.1, 3.7, 4.3, 4.9, 5.5, and 6.2 cm. The net was anchored on shore with the smallest mesh in the shallowest water and was deployed along the bottom perpendicular to the shoreline. This net was scanned continually and any fish captured were removed at 20-min intervals. If no fish were captured by nightfall, the net was left in place overnight and checked the following morning. Visual searches for amphibians were conducted from the raft and from shoreline areas.

Macroinvertebrates in the littoral zone of each lake were sampled by conducting multiple sweeps with a D-net (mesh size = 1 mm) over a 30-min period. Occasionally, sampling was done over shorter time periods when macroinvertebrates were extremely abundant. D-net sweeps followed bottom contours and sampled epibenthic, water column, and surficial sediment habitats that could be reached from shore. All habitat types were included, which consisted almost exclusively of silt-covered rocks with sand and silt between the rocks. Macroinvertebrates were sorted from debris and sediments in the field and then preserved in 70% ethanol. Macroinvertebrates were identified at 12–25× under a dissecting microscope using keys in Merritt and Cummins (1984) and Thorp and Covich (1991). Insects (other than chironomids), mollusks, and crustaceans were identified to genus. Chironomids were identified to tribe or subfamily, and mites were identified as the subclass Acari.

Zooplankton were sampled from a rubber raft by taking vertical tows with a plankton net (29.5 cm diameter, 40 µm mesh) from the deepest part of each lake at mid-day. The net was repeatedly lowered to the bottom and then retrieved until substantial numbers of zooplankton were present in samples. Filtered volumes for zooplankton samples were calculated assuming a net efficiency of 50% (Walters and Vincent 1973). Zooplankton samples were preserved in 5% formalin. In the laboratory, zooplankton samples were rinsed on a 45-µm sieve and then washed and diluted with water in a beaker. Subsamples (1 mL) were removed from the diluted sample with a wide-bore pipette, and subsamples of zooplankton were identified and counted in a Sedgewick–Rafter cell at 40× under a compound microscope. Depending on the abundance of zooplankton, from 1% to entire samples were counted. Microcrustaceans were identified using Edmondson (1959) and rotifers were identified using Stemberger (1979).

Water samples were collected by hand from lake outlets for analyses of pH, acid-neutralizing capacity (ANC), specific conductance, major ions, and aluminum. Samples were collected by entirely filling high-density polyethylene bottles that had been rinsed with deionized water. Sample aliquots for field determinations of pH and specific conductance and for laboratory determinations of ANC were simply decanted into bottles, sealed, and kept in the dark and cool (<10°C) until analysis. An aliquot for Cl, NO_3, SO_4, Ca, Mg, Na, and K was filtered through a 0.45 µm pore polycarbonate filter membrane into a bottle, sealed, and kept cool. An aliquot for total Al was filtered through a 0.1 µm pore polycarbonate filter, acidified with purified nitric acid, and sealed in an acid-leached bottle.

pH and specific conductance were measured using a Fisher Accumet 1000 pH meter with Accuphast glass electrode and a portable digital conductivity meter calibrated with National Institute for Standards and Testing conductivity standards. ANC was determined by incremental titration with 0.1 N HCl (Gran titration; Talling 1973). The anions Cl, NO_3, and SO_4 were analyzed using ion chromatography (Dionex AS4A column, sodium bicarbonate eluent). The cations Al, Ca, Na, Mg, and K were analyzed by atomic absorption. For greater sensitivity, a graphite furnace was used to atomize Al for atomic absorption analysis. Maximum lake depth was measured by plumb line from a raft.

Statistical analyses

We tested for normality and homogeneity of variances of data using Shapiro–Wilk and F tests. Because these assumptions were sometimes not met, we present the results of nonparametric tests for most comparisons, including the Wilcoxon two-sample test for comparing two groups and the Kruskal–Wallis test or ANOVA on ranked values followed by Tukey's HSD test for multiple comparisons. Our analyses, however, showed that parametric and nonparametric tests produced nearly identical results. Fisher's exact test was used to examine associations between the presence–absence of macroinvertebrate, zooplankton, and amphibian taxa and lake acidity (acidic vs. non-acidic) or the presence–absence of fish. Principal components analysis was used on the relative (macroinvertebrates) or absolute (limnetic zooplankton) abundances of common taxa (present in >5 lakes), and principal component scores for the three lake categories (acidic, fish, and non-acidic, fishless) were compared using one-way ANOVAs and Tukey's HSD tests. Correlation or regression analyses were used to relate zooplankton abundance or species richness and macroinvertebrate species richness to lake pH. Data on the relative abundances of macroinvertebrate taxa were angularly (arcsine square root) transformed and data on the absolute abundances of zooplankton taxa were $\log(x + 1)$ transformed before analyses to meet assumptions of parametric tests. All statistical tests were two-tailed, $\alpha = 0.05$, unless otherwise stated.

Results

Synoptic survey

The 104 surveyed lakes ranged in pH from 5.0 to 9.3 (median = 7.15) and included 10 lakes with pH < 6.0 (Fig. 2). Lakes ranged in conductivity from 2 to 102 µS/cm (median = 15 µS/cm), in elevation from 3130 to 3675 m (median = 3438 m), in estimated maximum depth from <0.5 to >5 m (median = 3.0 m), and in area from 0.03 to 30.5 ha (median = 0.31 ha). Acidic lakes had significantly higher conductivities than non-acidic lakes (medians = 35.5 and 14.8 µS/cm, respectively; Wilcoxon test, $p = 0.002$), whereas acidic lakes did not differ from non-acidic lakes in elevation, lake area, or maximum depth (Wilcoxon tests).

Golden trout (*Oncorhynchus mykiss aguabonita*), brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss irideus*), or brown trout (*Salmo trutta*) were found in 18 of the 104 lakes. Trout were absent from all 10 lakes with pH < 6 but were also absent from 76 of the 94 lakes with pH > 6 (Fisher's exact test on trout presence vs. absence in acidic vs. non-acidic lakes, $p = 0.20$; Fig. 2). Lakes containing trout were lower in elevation, larger in area, and deeper than lakes lacking trout. Median elevation was 3285 m in fish lakes and 3470 m in fishless lakes (Wilcoxon test, $p < 0.001$), and trout were not found in the 27 lakes above 3515 m elevation. Median lake area was 1.64 ha in fish

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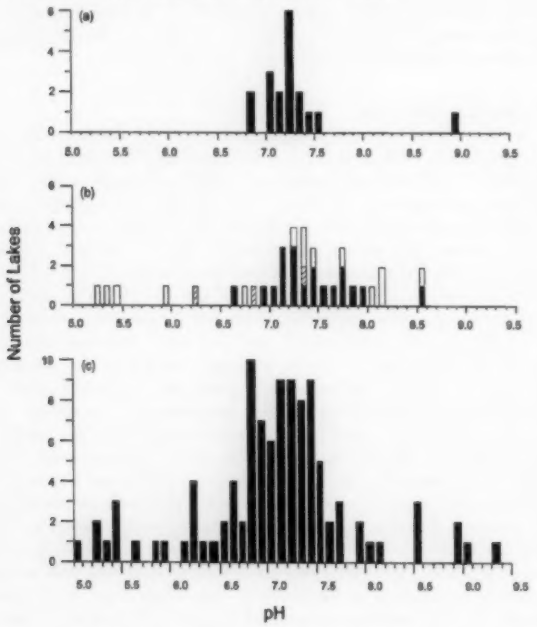
Fig. 2. Frequency distribution of pH in the synoptic survey. (*a*) Lakes where trout were observed (n = 18). (*b*) Lakes where yellow-legged frog (*Rana muscosa*) tadpoles and adults were observed (n = 36). Solid bars represent lakes containing both tadpoles and adults (n = 19); hatched bars represent lakes with tadpoles only (n = 3); and open bars represent lakes with adults only (n = 14). (*c*) All lakes surveyed (n = 104).



lakes and 0.26 ha in fishless lakes (Wilcoxon test, p = 0.001) and median estimated maximum depth was >5 m in fish lakes and 2.5 m in fishless lakes (Wilcoxon test, p = 0.020). Among non-acidic lakes, conductivity was higher in lakes containing fish (median = 23.1 µS/cm) than in lakes lacking fish (median = 12.9 µS/cm; Wilcoxon test, p = 0.036), but pH did not differ between fish and fishless lakes.

Amphibians observed in lakes were the tadpoles and adults of the mountain yellow-legged frog (*Rana muscosa*) and the tadpoles of the Pacific treefrog (*Hyla regilla*). Tadpoles of the yellow-legged frog were found in 22 lakes (19 with adults), and adults alone were found in 14 additional lakes (Fig. 2). In general, adults were found over a wider range of conditions (e.g., relative to presence of fish, pH, and depth) than tadpoles. Largely, tadpoles did not occur where fish were present. Tadpoles were found in only one of 18 trout lakes and 21 of 76 non-acidic (pH > 6) lakes lacking trout (Fisher's exact test, one-tailed, on presence–absence of tadpoles vs. presence–absence of trout, p = 0.03). In the single lake containing both fish and tadpoles (Lake N-3), tadpoles were found only in crevices in extensive shallow rocky areas. In contrast with tadpoles, the distribution of adults was not related to the presence of fish (present in 4 of 18 trout lakes and 25 of 76 non-acidic, fishless lakes (Fisher's exact test, p = 0.57)).

Yellow-legged frog tadpoles were not observed in any of the 10 acidic lakes (pH < 6; Fig. 2) but were seen in 21 of the 76 non-acidic lakes that lacked fish (Fisher's exact test, one-tailed, on frog presence–absence vs. acidic–non-acidic lakes, p = 0.051). When examining fishless lakes with estimated depths ≥ 1.5 m (approximate minimum depth required for overwintering tadpoles; Bradford 1989), tadpoles occurred in 0 of 8 acidic lakes but 20 of 57 non-acidic lakes (Fisher's exact test, one-tailed, p = 0.043). In contrast, yellow-legged frog adults were found in both acidic lakes (4 of 10) and non-acidic, fishless lakes (25 of 76) (Fisher's exact test, p = 0.73).

Among fishless, non-acidic lakes, the occurrence of yellow-legged frog tadpoles was significantly related to depth (Wilcoxon test, p = 0.02), whereas the occurrence of adults was not. Yellow-legged frog tadpoles were found only in lakes having maximum depths ≥ 1.5 m, whereas adult frogs were found in lakes as shallow as 0.5 m and less. Among fishless, non-acidic lakes, the occurrence of yellow-legged frog tadpoles and adults was not related to pH, conductivity, elevation, or lake area (Wilcoxon tests).

Pacific treefrog tadpoles were collected from six non-acidic lakes and from one acidic lake (pH = 5.96). None of these lakes contained fish.

Detailed survey

Physical–chemical conditions and trout distribution

The 33 lakes ranged in pH from 4.78 to 8.61 (median = 6.98), in conductivity from 3 to 126 µS/cm (median = 31.2 µS/cm), in elevation from 3130 to 3672 m (median = 3470 m), in area from 0.12 to 30.5 ha (median = 1.4 ha), and in maximum depth from 0.3 to 10.0 m (median = 2.6 m). All four trout species were represented among the seven lakes with fish. Trout occurred only in non-acidic lakes over a relatively narrow range of lake pH (6.9 to 7.5) in comparison with a total range of 4.8 to 8.6.

Among the three lake types (i.e., acidic lakes, non-acidic lakes with fish, and non-acidic lakes without fish), differences were not observed for elevation and concentrations of Cl and Ca (Table 1). However, ANC was lower, and concentrations of NO_3, SO_4, NH_4, Mg, Na, K, and Al were higher, in acidic lakes than in at least one of the non-acidic lake types (i.e., fish or fishless). Lake area and depth were significantly greater in lakes with fish than in non-acidic lakes lacking fish. Chemical conditions did not differ between fish and fishless, non-acidic lakes.

Amphibians

Yellow-legged frog tadpoles were observed in 12 lakes (10 with adults), and adults alone were observed in an additional 8 lakes. Tadpoles occurred in a greater proportion of lakes in the detailed survey than in the synoptic survey simply because most of the shallowest (<1 m) lakes, which lacked tadpoles, were excluded from the detailed survey. As in the synoptic survey, tadpoles were generally absent where trout were present. However, this pattern was not significant (Fig. 3*a*; Fisher's exact test, p = 0.09) because the single lake containing both tadpoles and fish was included in the detailed survey. In contrast with tadpoles, the distribution of adults was not related to the presence of fish (Fig. 3*a*; Fisher's exact test, p = 0.67).

Tadpole distribution was significantly related to lake acidity (Fig. 3*c*). Tadpoles were not observed in any of the 8

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Table 1. Physical–chemical characteristics of acidic lakes (Acidic) and non-acidic lakes containing fish (Fish) or lacking fish (Fishless) sampled in the detailed survey.

	Lake type			Significant differences
	Acidic	Fish	Fishless	
n	8	7	18	
Elevation (m)	3406	3390	3467	
	(53)	(42)	(22)	
Lake area (ha)	2.0	8.8	1.7	A=FL<F
	(0.7)	(4.1)	(0.7)	
Depth (m)	2.1	5.3	2.7	A=FL<F
	(0.5)	(1.0)	(0.5)	
pH	5.2	6.9	6.9	A<FL=F
	(0.2)	(0.1)	(0.1)	
ANC (μequiv./L)	−1.7	82.9	106.9	A<F=FL
	(2.6)	(11.0)	(24.0)	
Conductivity (μS/cm)	56.1	26.6	42.6	A>F
	(6.4)	(3.6)	(10.0)	
Cl (μequiv./L)	5.9	3.8	6.0	
	(0.8)	(0.4)	(1.1)	
NO_3 (μequiv./L)	14.2	3.2	5.1	A>F=FL
	(2.5)	(1.3)	(1.9)	
SO_4 (μequiv./L)	416.5	134.7	212.2	A>F=FL
	(61.0)	(30.0)	(61.8)	
NH_4 (μM)	0.6	0.2	0.6	A>F
	(0.1)	(0.1)	(0.2)	
Ca (μequiv./L)	218.4	174.3	278.5	
	(17.1)	(24.1)	(60.7)	
Mg (μequiv./L)	100.4	21.7	28.7	A>F=FL
	(16.8)	(4.4)	(5.9)	
Na (μequiv./L)	43.1	28.4	42.8	A>FL
	(4.8)	(5.4)	(17.1)	
K (μequiv./L)	17.8	6.9	10.7	A>F=FL
	(2.2)	(0.8)	(1.6)	
Al (μM)	13.04	0.81	1.19	A>F=FL
	(3.69)	(0.25)	(0.20)	

Note: *n* is the number of lakes in each category; numbers in the body of the table are mean values and numbers in parentheses are SEs for means. ANC refers to acid-neutralizing capacity. The right column summarizes statistically significant differences among lake types (A, acidic; F, non-acidic containing fish; FL, non-acidic without fish) based on ANOVAs on ranked values and Tukey's HSD test, $\alpha = 0.05$. When only two lake types are listed in the right column, the third lake type is not significantly different from the two listed lake types.

acidic lakes (all lacked fish) but occurred in 11 of 18 non-acidic lakes lacking fish (Fisher's exact test, $p = 0.008$). Moreover, pH and ANC of fishless lakes lacking tadpoles was lower than in fishless lakes containing tadpoles (Table 2). Conductivity and concentrations of NO_3, Ca, Mg, and Al were higher in lakes lacking tadpoles. Among non-acidic, fishless lakes ($n = 18$), none of the chemical or physical parameters differed between lakes containing ($n = 11$) and lacking tadpoles ($n = 7$; Wilcoxon tests).

In contrast with tadpoles, the distribution of adults was not significantly related to any chemical or physical parameters (Table 2). Adults were seen in lakes with pH as low as 5.0, occurring in 5 of 8 acidic lakes and 10 of 18 non-acidic lakes lacking fish. This difference between the distributions of tadpoles and adults relative to pH was conspicuous in areas containing both acidic and non-acidic lakes in close proximity. For example, both acidic Lake F-14 and nearby acidic Lake F-13N contained only adult frogs, whereas non-acidic Lake F-11, which was located 0.1 km downstream from Lake F-13N, contained both adults and tadpoles. Similarly, non-acidic Lake F-13S was separated from acidic Lake F-13N by a narrow causeway (ca. 25 m wide); both contained adults, but only the non-acidic lake contained tadpoles.

No individuals of the Pacific treefrog were found in lakes in the detailed survey, although they occurred in some unmapped ponds near these lakes.

Macroinvertebrates

Most common macroinvertebrate taxa showed relationships with the presence or absence of fish. Limnephilid caddis larvae (Limnephilidae: primarily *Desmona mono* and *Hesperophylax*), mayfly nymphs (Baetidae: *Baetis*, *Callibaetis*; Siphlonuridae: *Ameletus*; Heptageniidae: *Cinygmula*), dytiscid beetles (Dytiscidae: *Agabus*, *Deronectes*, *Hydaticus modesto*, *Hydroporus*, *Hydrovatus*, *Rhantus*), and corixids (Corixidae: *Graptocorixa*, *Hesperocorixa*, *Sigara*) were rare or absent in fish lakes but were commonly collected in non-acidic lakes lacking fish (Fisher's exact tests for these four groups, $p = 0.001$ to 0.026; Fig. 3*a*). Chironomids, including Chironomini, Orthocladiinae, Tanypodinae, and Tanytarsini, were collected from lakes containing and lacking fish. Among rarer taxa (i.e., occurring in 3 to 6 lakes), backswimmers (*Notonecta*) were only collected in lakes lacking fish, the caddis larvae of *Polycentropus variegatus* were collected only in lakes containing fish, and alderfly larvae (*Sialis latreille*), acarids, and fingernail clams (*Pisidium*) were collected from both fish and fishless lakes. Amphipods (*Hyallela azteca*), adult whirligig beetles (*Gyrinus punctellus*), water striders (*Gerris*), and the larvae of a stonefly (*Isoperla*), the limnephilid caddisfly *Ecclisomyia*, a damselfly (*Enallagma*), a mosquito (*Culex*), and a dixid (*Dixa*) were each collected from only one or two lakes.

Of the common macroinvertebrate taxa, only limnephilid caddis larvae seemed to show any relationship with pH, being found in only 37% of the acidic lakes but 81% of the non-acidic lakes lacking fish (Fisher's exact test, $p = 0.047$; Fig. 3*c*). Within this family, *Hesperophylax* was not collected from acidic lakes but was collected from half of the non-acidic lakes without fish (Fisher's exact test, $p = 0.018$), whereas *Desmona mono* was present in both acidic and non-acidic lakes (Fisher's exact test, $p = 0.66$). Most other common taxa, including siphlonurid mayflies (*Ameletus*), Dytiscidae, Corixidae, and Chironomidae, were collected in similar frequencies in acidic and non-acidic lakes (Fig. 3*c*). Among rare taxa, baetid and heptageniid mayflies, *Sialis latreille*, *Notonecta*, sphaerid clams, and amphipods were not collected from acidic lakes but were collected from a small number of non-acidic lakes.

A principal components analysis (PCA) on the angularly transformed relative abundances of common macroinvertebrate taxa tended to confirm these patterns (Fig. 4*a*). Principal components axes 1 and 2 accounted for 26% and 22%, respectively, of the total variation in the macroinvertebrate data set. Scores for principal components axis 1, which were positively correlated with the transformed relative abun-

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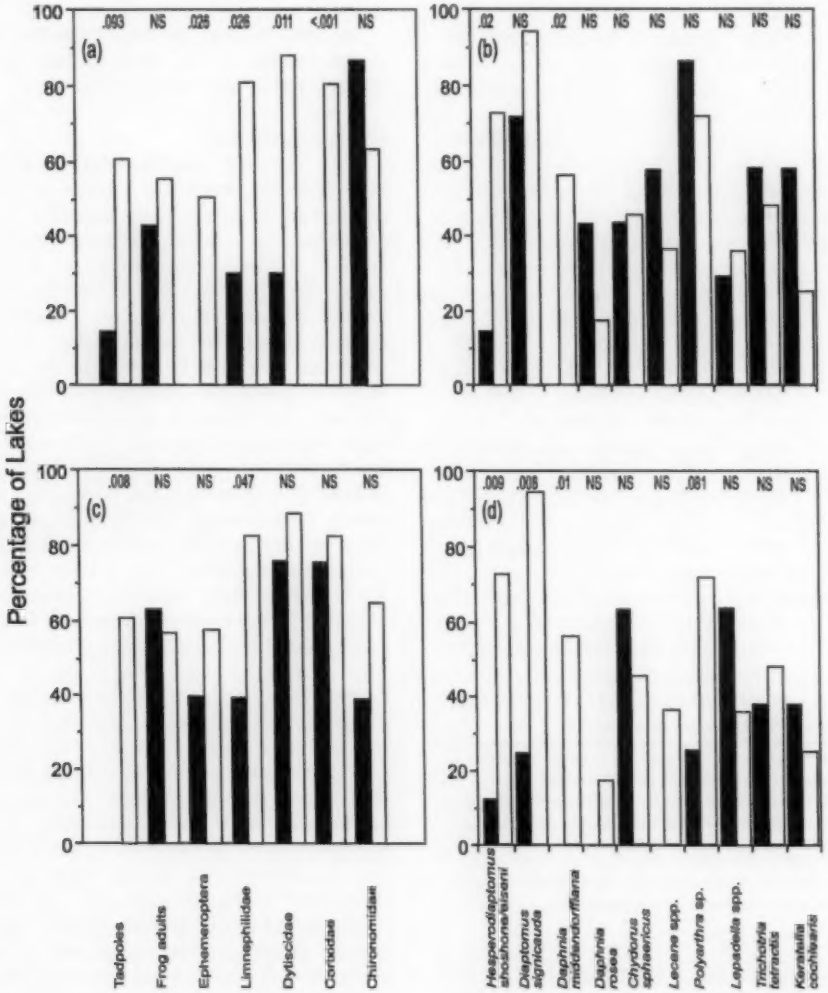
Fig. 3. Taxa in detailed survey. (*a*) Among non-acidic lakes (n = 23 to 25), the percentages of lakes containing fish (n = 7; solid bars) and lacking fish (n = 16 to 18; open bars) that were inhabited by mountain yellow-legged frog tadpoles and adults and macroinvertebrate taxa. (*b*) Among non-acidic lakes (n = 24 to 25), the percentages of lakes containing fish (n = 7; solid bars) and lacking fish (n = 17 to18; open bars) that were inhabited by designated zooplankton taxa. (*c*) Among fishless lakes (n = 24 to 26), the percentages of acidic lakes (pH < 6.0; n = 8; solid bars) and non-acidic lakes (pH > 6.0; n = 16 to 18; open bars) containing frogs and macroinvertebrate taxa. (*d*) Among fishless lakes (n = 25 to 26), the percentages of acidic lakes (pH < 6; n = 8; solid bars) and non-acidic lakes (pH > 6; n = 17 to 18; open bars) containing zooplankton taxa. Probability levels for Fisher's exact test are given at the top; NS, p values > 0.1.



dances of dytiscids, corixids, and ephemeropterans and negatively correlated with transformed chironomid relative abundance, were significantly different between lakes containing versus lacking fish (ANOVA, $F_{2,28}$ = 8.5, p = 0.001; acidic = non-acidic fishless > non-acidic fish, p < 0.05, Tukey's HSD). Principal components axis 2 was positively correlated with the transformed relative abundances of *Hesperophylax* and *Sialis* and negatively correlated with the transformed relative abundance of *Desmona*. Although the effect of lake type on the scores for this principal component was not statistically significant (ANOVA, $F_{2,28}$ = 2.0, p = 0.15), this axis tended to distinguish taxa that were absent from acidic lakes (*Hesperophylax, Sialis*) from a taxon for which relative abundance was higher in acidic than non-acidic lakes (*Desmona*).

Taxon richness was significantly higher in non-acidic fishless lakes than in acidic and fish lakes (non-acidic fishless: mean = 6.1, SE = 0.7, n = 16; acidic: mean = 3.8, SE = 0.4, n = 8; non-acidic fish: mean = 3.1, SE = 1.0, n = 7; Kruskal–Wallis tests, p = 0.024 and 0.037, respectively). For fishless lakes (n = 24), there was a significant direct relationship between taxon richness and pH (regression equation: richness = –2.21 + 1.19 pH; r^2 = 0.19; $F_{1,22}$ = 5.2, p < 0.032).

Zooplankton

The largest-bodied zooplankton taxa, i.e., *Hesperodiapto-*

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Table 2. Water chemistry of fishless lakes containing and lacking yellow-legged frog tadpoles or adults.

	Tadpoles			Adults	
	Present		Absent	Present	Absent
n	11		15	11	15
pH	7.28	*	6.29	6.72	6.70
	(0.21)		(0.29)	(0.33)	(0.28)
ANC (μequiv./L)	103	*	43.5	58.1	78.1
	(31)		(20.1)	(24.8)	(27.1)
Conductivity (μS/cm)	38.0	*	46.2	42.3	43.0
	(12.8)		(4.2)	(6.1)	(9.3)
Cl (μequiv./L)	5.1		6.6	7.2	5.1
	(0.7)		(1.3)	(1.8)	(0.5)
NO_3 (μequiv./L)	1.9	**	12.7	11.1	5.9
	(0.9)		(2.3)	(3.0)	(2.0)
SO_4 (μequiv./L)	228		319	247	306
	(96)		(50)	(60)	(75)
NH_4 (μM)	0.89		0.53	0.70	0.65
	(0.27)		(0.10)	(0.16)	(0.19)
Ca (μequiv./L)	257	*	262	262	259
	(96)		(28)	(40)	(69)
Mg (μequiv./L)	26.6	**	68.3	47.1	53.3
	(8.7)		(13.0)	(12.7)	(13.3)
Na (μequiv./L)	55.6		33.6	27.6	54.2
	(27.5)		(4.5)	(5.4)	(19.9)
K (μequiv./L)	10.7		14.4	11.3	14.0
	(2.2)		(1.9)	(2.0)	(2.0)
Al (μM)	1.18	*	8.46	6.17	4.50
	(0.24)		(2.76)	(3.31)	(1.83)

Note: Values are means (SEs). Asterisks between the groups indicate significance levels for Wilcoxon two-sample tests (* $p < 0.05$, ** $p < 0.01$). Other definitions are as in Table 1.

mus eiseni and *H. shoshone*, and *Daphnia middendorffiana* (maximum size > 2 mm) were rare or absent in fish lakes (14 and 0% of lakes, respectively) but were commonly collected in non-acidic lakes lacking fish (72 and 55% of lakes) (Fisher's exact tests, $p = 0.02$; Fig. 3*b*). *Daphnia rosea* and *Keratella cochlearis* tended to be collected more frequently in fish lakes than in non-acidic fishless lakes; however, these patterns were not significant (Fig. 3*b*). *Diaptomus signicauda, Chydorus sphaericus, Trichotria tetractis, Lecane* spp., *Lepadella* spp., and *Polyarthra* sp. were collected with similar frequencies from fish and fishless lakes. Many rare (three to six lakes) or littoral taxa, including the cladoceran *Alona* sp., and the rotifers *Hexarthra mira, Trichocerca capucina, Collotheca mutabilis, Keratella taurocephala*, and *Conochilus unicornis* were collected in lakes both containing and lacking fish; however, the cladoceran *Macrothrix hirsuticornis* was only collected from fishless lakes (five lakes). The cladocerans *Polyphemus pediculus, Holopedium gibberum, Bosmina longirostris, Scapholebris kingii*, and *Eurycercus lamellatus*, and the rotifers *Monostyla lunaris, Notholca labis*, and *Cephalodella* sp. were each collected from only one or two lakes.

Hesperodiaptomus eiseni, H. shoshone, and *Diaptomus signicauda* were rarely collected in acidic lakes (13–25% of lakes), and *Daphnia* spp. were absent in acidic lakes, but these microcrustaceans were frequently collected from non-acidic lakes lacking fish (72–94% of lakes) (Fisher's exact tests, $p = 0.002$ to 0.009; Fig. 3*d*). Correlations between the abundances of these taxa and pH for fishless lakes were significant; however, there was a lot of scatter in the data at higher pH ($r = 0.46$ to 0.59; Fig. 3*d*). The rotifer *Lecane* was not collected from acidic lakes; however, its low frequency of occurrence in non-acidic fishless lakes (35% of lakes) precluded statistical significance (Fisher's exact test, $p = 0.13$). *Polyarthra* sp. also tended to be collected more frequently in non-acidic than acidic lakes (Fig. 3*d*). Other common zooplankton taxa, including the cladoceran *Chydorus sphaericus* and the rotifers *Keratella cochlearis, Lepadella* spp., and *Trichotria tetractis*, were collected at similar frequencies in acidic and non-acidic, fishless lakes (Fig. 3*d*), and their densities were not significantly related to pH (examples in Fig. 5). Among rare species, *Macrothrix, Alona, Trichocerca, Keratella taurocephala*, and *Conochilus* were absent from acidic lakes but were present in a small number of non-acidic lakes (three to six lakes depending on the species), whereas *Collotheca* was collected from both acidic and non-acidic lakes. An unidentified rotifer, tentatively assigned to *Pompholyx* sp., was collected predominantly in acidic lakes (5 of 8 acidic lakes, 1 of 17 non-acidic fishless lakes; Fisher's exact test, $p = 0.006$).

A principal components analysis on log-transformed absolute abundances of common limnetic taxa tended to confirm these results (Fig. 4*b*). Principal components axes 1 and 2 accounted for 26% and 20%, respectively, of the total variation in the zooplankton data set. Lake type had a borderline effect on principal components axis 1 (ANOVA, $F_{2,28} = 2.25$, $p = 0.10$) and a highly significant effect on principal components axis 2 (ANOVA, $F_{2,28} = 6.6$, $p = 0.003$), with generally higher scores for both axes in non-acidic lakes than in acidic lakes (Tukey's HSD, $p < 0.05$). Taxa positively correlated with each of these axes were taxa that were rare or absent in acidic lakes (*Daphnia middendorffiana, Daphnia rosea, Hesperodiaptomus* spp., *Diaptomus signicauda, Conochilus unicornis, Keratella* spp.). Although the data were highly variable, taxa positively associated with principal components axis 1 (*Keratella, Daphnia rosea, Diaptomus signicauda, Conochilus unicornis*) were equally abundant in non-acidic fish lakes and fishless lakes, whereas mean abundances of the taxa negatively associated with principal components axis 1 (*Lepadella, Trichotria*) were higher in non-acidic fishless lakes than in acidic or fish lakes. Two of the taxa positively associated with principal components axis 2 (*Daphnia middendorffiana, Hesperodiaptomus* spp.) were virtually absent from acidic lakes or lakes containing fish but were relatively common in non-acidic fishless lakes.

Microcrustacean species richness increased significantly with increasing pH in fishless lakes (Fig. 6), whereas rotifer species richness did not. Species richness of both microcrustaceans and rotifers was not significantly affected by the presence of fish.

Discussion

Effects of acidity

This study indicates that the distributions and abundances of some aquatic animals are affected by natural lake acidity. Tadpoles, large-bodied microcrustaceans (*Daphnia, Diapto-*

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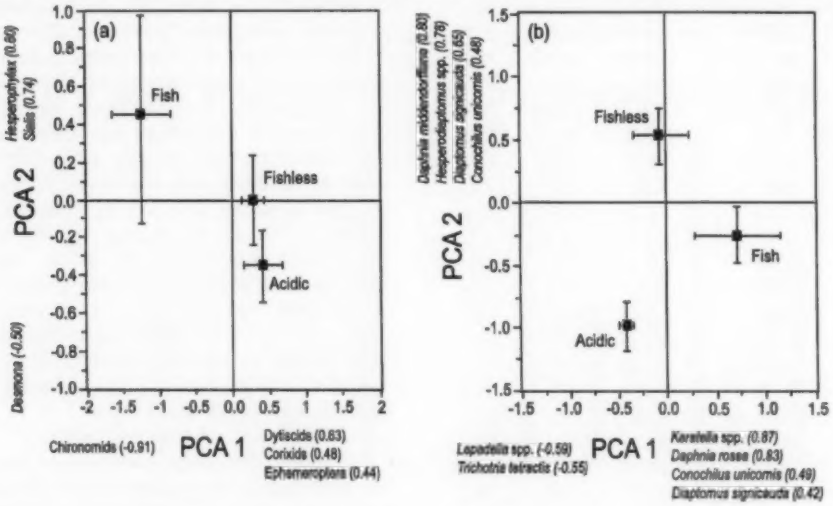
Fig. 4. Mean scores (± 1 SE) for principal components axes 1 and 2 for common taxa (i.e., present in >5 lakes) in the detailed survey. (*a*) Axes are derived for angularly transformed relative abundances of macroinvertebrate taxa for each of the three lake types (acidic and non-acidic with fish (Fish) and without fish (Fishless)). Taxa showing significant positive or negative association with each principal components axis are listed, and correlation coefficients (Pearson's *r*) are included in parentheses. (*b*) Axes are derived for log(x + 1)-transformed densities (no./m^3) of limnetic zooplankton taxa. Lake types and other designations are as in Fig. 4*a*.



mus), and the larvae of a species of limnephilid caddisfly (*Hesperophylax*) were rare or absent in acidic lakes but relatively common in non-acidic lakes. Based on differences in the distributions of tadpoles versus adult frogs noted in this study, it appears that larval amphibians are more sensitive to acid conditions than adults, consistent with results reported from other survey and experimental studies (Freda 1990). The absence of tadpoles from acidic lakes where adults were present also could have been owing to disruption of frog mating activities, site selection for breeding, embryonic development, or metamorphosis. Embryonic stages of many amphibians, including the mountain yellow-legged frog, are more sensitive to increased acidity than larvae (Freda 1990; Bradford et al. 1992) and transitional processes, such as egg hatching or metamorphosis, appear to be easily disrupted by acid stress (Clark and LaZerte 1985).

With the exception of the limnephilid caddis larva, *Hesperophylax*, the distributions of common macroinvertebrate taxa were unrelated to lake acidity. Previous survey and experimental studies in the Sierra also have found little relationship between the distributions or abundances of macroinvertebrates and pH; however, previous surveys only examined a restricted range of pH values (>6.3) and experimental studies examined responses of the infauna at the bottom of lake enclosures (Melack et al. 1989; Barmuta et al. 1990). Our survey results extend this lack of a relationship between macroinvertebrate distributions and lake acidity to a wider range of pH values and to epibenthic and water column taxa. Macroinvertebrate taxa identified as sensitive to acidic conditions in previous studies, such as baetid mayflies, amphipods, and sphaerid clams (Mills and Schindler 1986; Okland and Okland 1986), were not found in acidic lakes in the present study; however, their infrequent collection in non-acidic lakes precluded rigorous statistical testing. *Sialis* larvae are generally thought to be tolerant of acidic conditions but were only collected from five non-acidic lakes, and mayflies, in general, are thought to be sensitive to acidic conditions (Sutcliffe and Carrick 1973). However, the dominant mayfly genus collected from our study lakes, *Ameletus*, was found in several acidic lakes. Other studies have reported that siphlonurid mayflies, including species of *Ameletus*, are insensitive to acidic conditions (Rosemond et al. 1992). In general, it appears that macroinvertebrate taxa sensitive to acidic conditions are rare in High Sierra lakes, even those with circumneutral or alkaline pH. Nevertheless, macroinvertebrate taxon richness was lower in acidic lakes than in fishless, non-acidic lakes, a finding consistent with the significant positive correlation reported between macroinvertebrate taxon richness and pH in Sierra Nevada lakes in a previous study (Jenkins et al. 1994).

In contrast with macroinvertebrates, zooplankton assemblages appeared to show a greater variety of responses to increased acidity. Common microcrustacean taxa, such as *Hesperodiaptomus eiseni, H. shoshone, Diaptomus signicauda, Daphnia middendorffiana,* and *Daphnia rosea,* were rare or absent in acidic lakes (pH < 6) but were collected commonly in non-acidic lakes. There also appeared to be differences in the responses of these sensitive taxa: *Hesperodiaptomus shoshone* was collected in low densities from a lake with pH 5.3, *Diaptomus signicauda* was collected from lakes with pH 5.3 and 5.7, but the lowest pH for waters from which *Daphnia* was collected was 6.3. The cladocerans *Macrothrix hirsuticornis* and *Alona* sp. and the rotifers *Conochilus unicornis* and *Lecane* spp. were also absent in acidic waters but were collected from 5, 6, 5, and 10 non-acidic lakes, respectively. In contrast, the common chydorid cladoceran *Chydorus sphaericus* and a number of rotifers, including *Keratella cochlearis, Polyarthra* sp., *Trichotria tetractis*, and *Lepadella* spp., were collected in both acidic and non-acidic lakes. Previous surveys of High Sierra zooplankton

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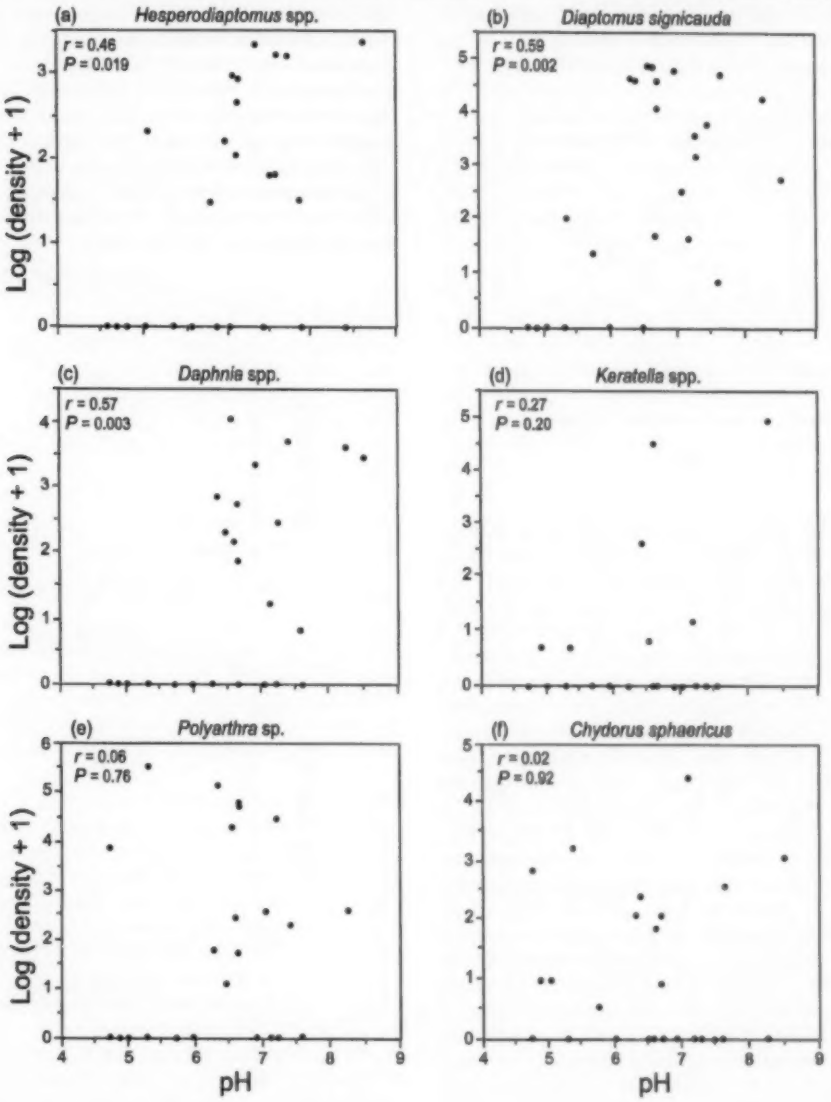
Fig. 5. Relationships between log-transformed abundances (no./m^3) of common zooplankton taxa and pH for fishless lakes sampled in the detailed survey (n = 25). r and P refer to Pearson's correlation coefficient and associated probability value, respectively.



assemblages (e.g., Stoddard 1987; Melack et al. 1989) found few relationships between the presence or abundances of zooplankton taxa and pH; however, these surveys did not include lakes with pH < 6.

Comparisons of our survey results with the results of previous small-scale experiments examining the effects of acid inputs on the survivorship and development of mountain yellow-legged frogs revealed some discrepancies. For example, although tadpoles were absent at pH < 6.0 in our survey, survivorship of embryos and tadpoles in the laboratory was not significantly affected by pH as low as 4.75 (Bradford et al. 1992). Developmental rates of embryos, however, were reduced at pH ≤ 5.25 in these experiments. The possibly greater sensitivity of early frog stages to acidic conditions in the field may stem from several factors. Many chemical species are negatively correlated with pH (Table 1), and concentrations of NO_3, Ca, Mg, and Al were significantly higher where tadpoles were absent. Possibly, these factors, rather than pH, may be directly affecting embryos or tadpoles in the field. For example, acidic lakes contained Al concentrations many times greater than levels used in the laboratory experiments, and aluminum can be toxic to amphibian embryos and larvae (Freda 1991). Acidic lakes contained a median of 13 μM aluminum (range: 2–25), whereas levels in laboratory experiments at similar pH were approximately 3 μM (Bradford et al. 1992). Other possible explanations include the following: one-time sampling in the field may have missed extreme pH depressions; only a restricted

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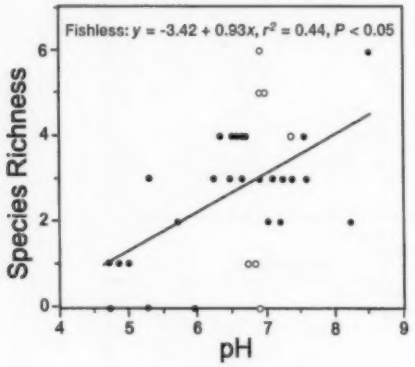
Fig. 6. Relationship between microcrustacean species richness and pH for all lakes in the detailed survey (n = 33). Open circles represent lakes containing fish; solid circles represent lakes lacking fish. The regression line was fitted by the procedure of least squares to data from fishless lakes only (n = 26).

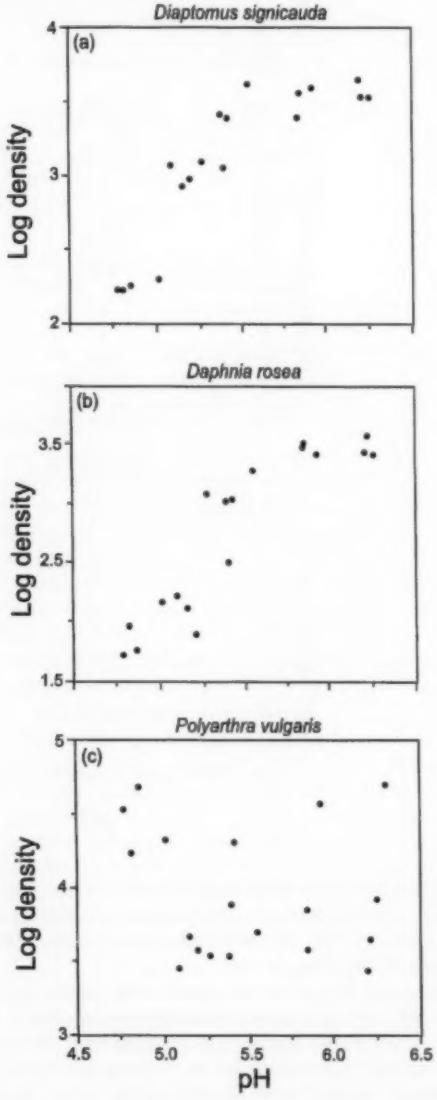


part of the mountain yellow-legged frog life cycle was examined in laboratory experiments (i.e., embryos and hatchling tadpoles); laboratory experiments were conducted at a "summertime" temperature of 15°C, whereas tadpoles overwinter under ice at 0 to 4°C for many months (Bradford 1989); and adults may choose not to breed in acidic waters.

In contrast with the discrepancies seen for amphibians, our survey results for zooplankton were nearly congruent with zooplankton responses to acid inputs in large experimental enclosures in a High Sierra lake (Emerald Lake, Barmuta et al. 1990; Melack et al. 1989). The survey suggested that *Daphnia* and *Diaptomus signicauda* were sensitive to pH < 6, whereas *Chydorus, Polyarthra*, and *Keratella* were relatively insensitive to acidity. Similarly, experimental manipulations of pH showed that *Diaptomus signicauda* and *Daphnia* declined in abundance when pH was reduced below 5.8–6.0, whereas *Chydorus sphaericus* and *Polyarthra* sp. were relatively unaffected by pH manipulations (Fig. 7). Furthermore, *Daphnia* seemed to be slightly more sensitive to acid inputs than *Diaptomus* in both our survey (Fig. 5) and in these experiments (Fig. 7). *Keratella* was unresponsive to pH in the survey but generally increased in abundance in enclosures as pH declined below 5.6 (Barmuta et al. 1990); however, it is difficult to specifically compare survey and experimental results because the dominant *Keratella* species was not the same in each case. *Keratella taurocephala* was the dominant species in the experiment, whereas *K. cochlearis* was the species typically collected in the survey; *K. taurocephala* is usually thought to be more tolerant of acidic conditions than *K. cochlearis* (Roff and Kwiatkowski 1977; Brezonik et al. 1993; Gonzalez and Frost 1994) but was only collected from three of the surveyed lakes (pH 6.53–6.91).

Our survey results corroborate an extensive literature documenting the high sensitivity of most species of *Daphnia* and many species of *Diaptomus* to acid inputs and the high tolerance of *Chydorus, Keratella*, and *Polyarthra* to acidic conditions (reviewed in Brett 1989). Our results are also consistent with literature showing positive relationships between microcrustacean species richness and pH (see review in Brett 1989). In contrast with previous studies, however, we found no relationship between rotifer species richness and pH (Roff and Kwiatkowski 1977). As with yellow-

Fig. 7. Relationships between log-transformed abundances (no./m^3) of three zooplankton taxa and pH in a field experiment (Barmuta et al. 1990) for comparison with data for the same or related taxa in the detailed survey (see Fig. 5). The field experiment was conducted for 35 days in 18 polyethylene enclosures (each 7.6 m^3) that extended from the bottom to the surface of a High Sierra lake. Nitric and sulphuric acid were added in varying amounts to enclosures to create six pH levels, with three replicate enclosures at each level. Data shown are mean abundances of designated zooplankton taxa in each enclosure versus mean pH of each enclosure after acidification over the duration of the experiment.



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legged frog tadpoles, it is possible that chemical parameters other than pH affected the distributions and abundances of macroinvertebrates and zooplankton. Because the concentrations of a number of chemical species are correlated strongly with pH, pH can be used as an index of the amalgam of chemical factors that are likely to change with increasing acidity and that may affect, alone or together, the distributions and abundances of aquatic animals. In addition, our survey results were congruent with the results of field experiments where primarily proton concentrations were manipulated, indicating that differences in hydrogen ion concentrations could explain differences in species composition and abundance among lake types.

Fish distributions within the study area appear to be related primarily to historical stocking patterns, rather than lake acidity. Trout were originally absent from most waters of the High Sierra, including all lakes in the study area (Knapp 1996). California Department of Fish and Game records show that stocking occurred between 1936 and 1979 in at least six lakes in the B, C, D, and E basins. We observed fish primarily in large deep lakes in these basins and in a few connecting lakes that lacked physical barriers to dispersal from these large lakes. There are no stocking records for fish in the F, L, O, and P drainages, where fish are currently absent. The only acidic lake that we know was stocked is Lake C-24, a lake currently devoid of fish. This lake was planted with rainbow trout at least five times between 1946 and 1979. Because this lake lacks inflowing and outflowing streams, which are necessary for spawning, and because rainbow trout are unlikely to live over 13 years, the absence of trout from this lake could be owing to lack of spawning habitat rather than acidic conditions (Moyle et al. 1996).

The results of this and other studies indicate that acidic conditions may restrict the distributions of larval amphibians, large microcrustaceans, and a few macroinvertebrates and reduce the species richness of microcrustaceans and macroinvertebrates. Currently, however, acidity has a very limited influence on aquatic animals in the High Sierra simply because acidic lakes are extremely rare. Of the approximately 4000 lakes in the Sierra Nevada, the 10 acidic lakes in this study are the only ones known to have been acidified either by natural or anthropogenic sources (Melack et al. 1985; Landers et al. 1987; Melack and Stoddard 1991; Bradford et al. 1994*b*). Moreover, the pH of lakes in the Sierra Nevada very rarely dips below 5.6 during snowmelt (Melack et al. 1989; Stoddard 1995). However, our survey results do provide an indication of how aquatic biodiversity in the Sierra will respond to long-term increases in anthropogenic acidification.

Effects of introduced fish

The results of the present study suggest that the introduction of fish has had profound effects on the structure and composition of faunal assemblages in High Sierra lakes. Large and (or) mobile, conspicuous taxa, including tadpoles, large-bodied microcrustacean zooplankton (*Hesperodiaptomus, Daphnia middendorffiana*), and many epibenthic or limnetic macroinvertebrates (baetid and siphlonurid mayflies, notonectids, corixids, limnephilid caddis larvae, and dytiscid beetles), were rare or absent in lakes containing fish but were commonly collected in lakes lacking fish. The disappearance of the mountain yellow-legged frog from many parts of the Sierra may be owing to the widespread introduction of trout to Sierran lakes (Bradford 1989; Bradford et al. 1993). Frog disappearances may have occurred both by direct fish predation on vulnerable life stages (e.g., tadpoles) and by isolation of remaining populations from one another (Bradford et al. 1993). An extensive literature documents that large-bodied zooplankton species are generally found only in fishless lakes, whereas small species dominate in lakes containing fish (Brooks and Dodson 1965; Walters and Vincent 1973; Zaret 1980; Stoddard 1987; Melack et al. 1989; Northcote 1988). Similarly, macroinvertebrate taxa that are conspicuous owing to their size, activity, and (or) exposure are often rare in lakes containing fish. Large, active, and epibenthic–limnetic macroinvertebrates (e.g., large mayflies, epibenthic odonates, hemipterans, limnephilid caddis larvae, dytiscid beetles) are often reduced or eliminated by fish predation, shifting dominance to smaller or more cryptic taxa (e.g., chironomids, oligochaetes) (Bendell and McNicol 1987; Northcote 1988; Evans 1989; Hoffman et al. 1996).

Trout have been introduced to the vast majority of lakes in the Sierra Nevada where fish formerly did not occur (Moyle et al. 1996; Knapp 1996). Data presented in Bahls (1992) indicate that 63% of high mountain lakes in California contain introduced fish, including 97% of the large lakes (>2 ha). About half of the Sierran lakes are regularly stocked with non-native fish. Our study and others indicate that introduced trout eliminate or greatly reduce the numbers of large, mobile, and epibenthic–limnetic taxa, including amphibians and invertebrates. At the current time, the widespread introduction of non-native fish appears to be affecting profoundly the native biodiversity of aquatic ecosystems in the High Sierra.

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References

Anderson, R.S. 1980. Relationships between trout and invertebrate species as predators and the structure of the crustacean and rotiferan plankton in mountain lakes. *In* Evolution and ecology of zooplankton communities. *Edited by* W.C. Kerfoot. University Press of New England, Hanover, N.H. pp. 635–641.

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Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Science, **66**: 183–193.

Barmuta, L.A., Cooper, S.D., Hamilton, S.K., Kratz, K.W., and Melack, J.M. 1990. Responses of zooplankton and zoobenthos to experimental acidification in a high-elevation lake (Sierra Nevada, California, U.S.A.). Freshwater Biol. **23**: 571–586.

Bendell, B.E., and D.K. McNicol. 1987. Fish predation, lake acidification, and the composition of aquatic insect assemblages. Hydrobiologia, **150**: 193–202.

Bradford, D.F. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implication of the negative effect of fish introductions. Copeia, 1989: 775–778.

Bradford, D.F., Swanson, C., and Gordon, M.S. 1992. Effects of low pH and aluminum on two declining species of amphibians in the Sierra Nevada, California. J. Herpetol. **26**: 369–377.

Bradford, D.F., Graber, D.M., and Tabatabai, F. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Conserv. Biol. **7**: 882–888.

Bradford, D.F., Cooper, S.D., Brown, A.D., Jenkins, T.M., Jr., Kratz, K., and Sarnelle, O. 1994*a*. Distribution of aquatic animals relative to naturally acidic waters in the Sierra Nevada. Final Report, Contract No. A132-173, California Air Resources Board, Sacramento.

Bradford, D.F., Gordon, M.S., Johnson, D.F., Andrews, R.D., and Jennings, W.B. 1994*b*. Acidic deposition as an unlikely cause for amphibian population declines in the Sierra Nevada, California. Biol. Conserv. **69**: 155–161.

Brett, M.T. 1989. Zooplankton communities and acidification processes (a review). Water, Air, Soil Pollut. **44**: 387–414.

Brezonik, P.L., Eaton, J.R., Frost, T.M., Garrison, P., Kratz, T.K., Mach, C.E., McCormick, J.H., Perry, J.A., Rose, W.J., Sampson, C.J., Shelley, B.C.L., Swenson, W.A., and Webster, K.E. 1993. Experimental acidification of Little Rock Lake, Wisconsin: chemical and biological changes over the pH range 6.1 to 4.7. Can. J. Fish. Aquat. Sci. **50**: 1101–1121.

Brooks, J.L., and Dodson, S.I. 1965. Predation, body size, and composition of plankton. Science (Washington), **150**: 28–35.

Clark, K.L., and LaZerte, B.D. 1985. A laboratory study of the effects of aluminum and pH on amphibian eggs and tadpoles. Can. J. Fish. Aquat. Sci. **42**: 1544–1551.

Edmondson, W.T. (*Editor*). 1959. Freshwater biology. 2nd ed. John Wiley and Sons, Inc., New York.

Evans, R.A. 1989. Responses of limnetic insect populations of two acidic, fishless lakes to liming and brook trout (*Salvelinus fontinalis*) introductions. Can. J. Fish. Aquat. Sci. **46**: 342–351.

Freda, J. 1990. Effects of acidification on amphibians. *In* Biological effects of changes in surface water acid–base chemistry. *Edited by* J.P. Baker, D.P. Bernard, S.W. Christensen, M.J. Sale, J. Freda, K. Heltcher, D. Marmorek, L. Rowe, P. Scanlon, G. Suter, W. Warren-Hicks, and P. Welbourn. State-of-Science/Technology Report 13, National Acid Precipitation Program, Washington, D.C. pp. 114–129.

Freda, J. 1991. The effects of aluminum and other metals on amphibians. Environ. Pollut. **71**: 305–328.

Gonzalez, M.J., and Frost, T.M. 1994. Comparisons of laboratory bioassays and a whole-lake experiment: rotifer responses to experimental acidification. Ecol. Appl. **4**: 69–80.

Havens, K.E. 1993. Pelagic food web structure in Adirondack Mountain, U.S.A., lakes of varying acidity. Can. J. Fish. Aquat. Sci. **50**: 149–155.

Hoffman, R.L., Liss, W.J., Larson, G.L., Deimling, E.K., and Lomnicky, G.A. 1996. Distribution of nearshore macroinvertebrates in lakes of the Northern Cascade Mountains, Washington, U.S.A. Arch. Hydrobiol. **136**: 363–389.

Jenkins, T.M. Jr., Knapp, R.A., Kratz, K.W., and Cooper, S.D. 1994. Aquatic biota in the Sierra Nevada: current status and potential effects of acid deposition on populations. Final report, Contract No. A932-138, California Air Resources Board, Sacramento.

Knapp, R.A. 1996. Non-native trout in natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. *In* Sierra Nevada Ecosystem Project: final report to Congress. Vol. III. Assessments, commissioned reports, and background information. University of California, Centers for Water and Wildland Resources, Davis. pp. 363–407.

Landers, D.H., Ellers, J.M., Brakke, D.F., Overton, W.S., Keller, P.E., Silverstein, M.E., Schonbrod, R.D., Crowe, R.E., Linthurst, R.A., Omernik, J.M., Teague, S.A., and Meier, E.P. 1987. Characteristics of lakes in the western United States. Vol. 1. Population descriptions and physico-chemical relationships. U.S. Environmental Protection Agency, EPA-600/3-86/054a.

Locke, A. 1992. Factors influencing community structure along stress gradients: zooplankton responses to acidification. Ecology, **73**: 903–909.

Magnuson, J.J., Baker, J.P., and Rahel, E.J. 1984. A critical assessment of effects of acidification on fisheries in North America. Phil. Trans. R. Soc. Lond. B, **305**: 501–516.

Mahood, G., and Gansecki, C. 1993. Geologic controls of natural acidification of alpine lakes in the eastern Sierra Nevada. Final Report, Contract No. A132-173, California Air Resources Board, Sacramento.

Melack, J.M., and Stoddard, J.L. 1991. Sierra Nevada, California. *In* Acidic deposition and aquatic ecosystems: regional case studies. *Edited by* D.F. Charles. Springer-Verlag, New York. pp. 503–530.

Melack, J.M., Stoddard, J.L., and Ochs, C.A. 1985. Major ion chemistry and sensitivity to acid precipitation of Sierra Nevada lakes. Water Resour. Res. **21**: 27–32.

Melack, J.M., Cooper, S.D., Jenkins, T.M., Jr., Barmuta, L., Hamilton, S., Kratz, K., Sickman, J., and Soiseth, C. 1989. Chemical and biological characteristics of Emerald Lake and the streams in its watershed, and the responses of the lake and streams to acidic deposition. Final Report, Contract No. A6-184-32, California Air Resources Board, Sacramento.

Merritt, R.W., and Cummins, K.W. (*Editors*). 1984. An introduction to North American aquatic insects. 2nd ed. Kendall-Hunt, Dubuque, Iowa.

Mills, K.H., and Schindler, D.W. 1986. Biological indicators of lake acidification. Water, Air, Soil Pollut. **30**: 779–789.

Moore, J.G. 1963. Geology of the Mt. Pinchot quadrangle, southern Sierra Nevada, California. U.S. Geological Survey Bull. 1130, Washington, D.C.

Moyle, P.B., Yoshiyama, R.M., and Knapp, R.A. 1996. Status of fish and fisheries. Sierra Nevada Ecosystem Project: final report to Congress. Vol. II. Assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources, Davis. pp. 953–973.

Northcote, T.G. 1988. Fish in the structure and function of freshwater ecosystems: a top-down view. Can. J. Fish. Aquat. Sci. **45**: 376–393.

Okland J., and Okland, K.A. 1986. The effects of acid deposition on benthic animals in lakes and streams. Experimentia, **42**: 471–486.

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Roff, J.C., and Kwiatkowski, R.E. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. **55**: 899–911.

Rosemond, A.D., Reice, S.R., Elwood, J.W., and Elwood, P.J. 1992. The effects of stream acidity on benthic invertebrate communities in the south-eastern United States. Freshwater Biol. **27**: 193–209.

Stemberger, R.S. 1979. A guide to rotifers of the Laurentian Great Lakes. Final Report, Contract number R-804652, Environmental Monitoring and Support Laboratory, Office of Research and Development, U.S. Environmental Protection Agency, Cincinnati, Ohio.

Stoddard, J.L. 1987. Microcrustacean communities of high-elevation lakes in the Sierra Nevada, California. J. Plank. Res. **9**: 631–650.

Stoddard, J.L. 1995. Episodic acidification during snowmelt of high elevation lakes in the Sierra Nevada Mountains of California. Water, Air, Soil Pollut. **85**: 353–358.

Sutcliffe, D.W., and Carrick, T.R. 1973. Studies on the mountain streams of the English Lake District. I. pH, calcium, and the distribution of invertebrates in the River Duddon. Freshwater Biol. **3**: 437–462.

Talling, J.F. 1973. The application of some electrochemical methods to the measurement of photosynthesis and respiration in freshwaters. Freshwater Biol. **3**: 335–362.

Thorp, J.H., and Covich, A.P. (*Editors*). 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, Inc., San Diego.

Walters, C. J., and Vincent, R.E. 1973. Potential productivity of an alpine lake as indicated by removal and reintroduction of fish. Trans. Am. Fish. Soc. **102**: 675–697.

Whiting, M., Whitehead, D., Holmes, R., and Norton, S.A. 1989. Paleolimnological reconstruction of recent acidity changes in four Sierra Nevada lakes. J. Paleolimnol. **2**: 285–304.

Zaret, T.M. 1980. Predation and freshwater communities. Yale University Press, New Haven, Conn.

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Evaluation of side-aspect target strength and pulse width as potential hydroacoustic discriminators of fish species in rivers

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Abstract: Split-beam hydroacoustic data were collected on 98 tethered and 10 unrestrained Pacific salmon of known size to evaluate side-aspect target strength and pulse width as species discriminators in rivers. Pulse width was better able to discriminate chinook (*Oncorhynchus tshawytscha*) from sockeye salmon (*Oncorhynchus nerka*) than target strength, although its discriminatory power may have arisen from differences in behavior as well as size between species. Standard deviation of –12 dB pulse width was the best univariate size predictor and species discriminator among tethered fish but performed poorly among unrestrained fish at close ranges; mean pulse width at –12 dB performed well among both. Discriminatory power of all variables declined as the number of echoes per fish was reduced. Fish orientation, lateral movement, and spatial position of the fish in the beam affected hydroacoustic measurements. As fish moved more from side to side, and as fish orientation departed from full side aspect, target strength declined monotonically but mean pulse width increased and then declined. We show how some of the confounding effects of fish behavior on hydroacoustic measurements can be removed using corrections based on statistical models.

Résumé : Nous avons recueilli des données hydroacoustiques avec un système à faisceau partagé sur des saumons pacifiques (98 captifs et 10 libres) de taille connue pour évaluer la possibilité d'employer la dimension latérale de l'intensité de cible et la durée moyenne de l'impulsion comme discriminateurs spécifiques dans les cours d'eau. La durée de l'impulsion a donné de meilleurs résultats que l'intensité de cible pour différencier le quinnat (*Oncorhynchus tshawytscha*) du saumon rouge (*Oncorhynchus nerka*), mais son pouvoir discriminateur est peut-être dû à des différences de comportement et de taille entre les deux espèces. L'écart-type de –12 dB dans la durée de l'impulsion constituait le meilleur discriminateur spécifique et prédicteur de taille pour une seule variable parmi les poissons captifs, mais donnait des résultats médiocres à faible distance parmi les poissons libres; avec une durée moyenne de l'impulsion de –12 dB, les résultats étaient bons dans les deux groupes. Le pouvoir discriminateur de toutes les variables déclinait avec la baisse du nombre d'échos par poisson. L'orientation du poisson, le déplacement latéral et la position spatiale des poissons dans le faisceau affectaient les mesures hydroacoustiques. Quand les poissons se déplaçaient d'un côté à l'autre, et ne présentaient plus une orientation totalement latérale, l'intensité de cible baissait de façon monotone, mais la durée moyenne de l'impulsion augmentait d'abord pour baisser ensuite. Nous montrons en quoi certains des effets trompeurs du comportement des poissons sur les mesures hydroacoustiques peuvent être éliminés grâce à des corrections basées sur des modèles statistiques.

[Traduit par la Rédaction]

Introduction

Fisheries hydroacoustics are often limited by an inability to discriminate among fish taxa. This is particularly true for side-looking applications in rivers, where migrating fish are ensonified from a fixed transducer near the riverbank. Side-aspect target strength (TS) is related to fish size (Love 1969; Kubecka and Duncan 1998), but variable fish orientation and high levels of acoustic noise in rivers result in excessive measurement error. Attempts to use TS to discriminate among species have been unsuccessful (Johnston and Hopelain 1990; Vaught and Skvorc 1993), and riverine hydroacoustic applications have largely been limited to systems where a single species predominates (Gaudet 1990; Daum and Osborne 1996). Where abundance estimates are needed for several species migrating simultaneously, independent estimates of species composition have been required (e.g., Mesiar et al. 1990). Such estimates are often costly and imprecise.

On the Kenai River in southcentral Alaska, chinook salmon (*Oncorhynchus tshawytscha*) migrate concurrently with more numerous sockeye salmon (*Oncorhynchus nerka*). The two species differ greatly in size and migratory behavior; sockeye salmon average less than 60 cm in length and migrate primarily in shallow water close to the riverbank whereas chinook salmon often exceed 100 cm and migrate in deeper water near midchannel. Such differences led to attempts to count chinook salmon with side-looking dual-beam sonar (Eggers et al. 1995). To exclude as many sockeye as possible from counts of chinook salmon, only targets

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that exceeded minimum-range criteria and TS thresholds were counted. However, the efficacy of these techniques and the thresholds used were uncertain. Very few side-aspect TS data were available from salmonids of known size (Dahl and Mathisen 1983).

In the present study, side-aspect measurements were made on live, tethered chinook, sockeye, and coho salmon (*Oncorhynchus kisutch*) using split-beam techniques. Our experiments were initially designed to evaluate acoustic TS, a function of echo amplitude, as a discriminatory variable. However, other variables were also assessed, especially those describing the width (duration) of the acoustic echo. In this paper, we evaluate the effectiveness of side-aspect hydroacoustic measurements in general (TS, pulse width (PW), and combinations of both) as discriminators of fish species of different size in rivers. We also simulate the effect of sample size (number of echoes per fish) on discriminatory power, quantify the sensitivity of hydroacoustic measurements to spatial and behavioral factors, and demonstrate corrections for the confounding effects of these factors. Finally, we compare the tethered fish findings with those from 10 unrestrained chinook salmon of known size.

Methods

Three separate studies were conducted. First, we tethered 93 live chinook, sockeye, and coho salmon in front of a side-looking split-beam sonar. Second, to investigate the influence of orientation angle on hydroacoustic measurements, we tethered five sockeye salmon at multiple angles to the sonar beam. Both of these experiments were conducted in the Kenai River, where the water is glacially occluded. Third, we wished to obtain hydroacoustic data on free-swimming fish of known size and species to assess how well the tethered-fish findings applied to unrestrained fish. We conducted this study in a smaller, clearwater stream where we could visually observe marked fish.

Tethered fish

Hydroacoustic data on tethered fish were collected 19 June – 10 August 1995 and 21–22 July 1996 at kilometre 14 of the Kenai River. The site was within tidal influence, and water depth at midchannel varied from 3 to 8 m. The river is about 100 m wide at this location and the bottom substrate is silty mud. Water temperature ranged from 10 to 15°C. during the study.

Live chinook, sockeye, and coho salmon were captured with gill nets and held in live pens or totes until they could be deployed (Burwen et al. 1998). A cable tie was inserted through a small hole punched in the lower jaw. The cable tie was then attached to about 10 m of dacron fishing line that led to two 1.4-kg downrigger weights. Another section of dacron line (about 6 m in length) led from the weights to a buoy on the surface. The buoy, in turn, was attached with polypropylene line to an anchor upstream. Using this technique, we were able to isolate the fish from other scattering surfaces (i.e., lead weights, buoy, etc.).

In 1995, fish were tethered at approximately side aspect to the hydroacoustic beam (transducer was aimed perpendicularly to the river current) 13–41 m from the transducer. In 1996, tethered fish were positioned at several angles (aspects) to the beam. Fish were first stationed so that the transducer had to be aimed slightly upstream from perpendicular to the bank at 27–28 m range. Aspect could not be determined exactly because neither fish nor transducer was visible under the water. After several minutes of data collection, the transducer was panned downstream about 5° and the tether was lengthened until the fish was again centered in the beam. This process was repeated until the fish was no longer detectable above background noise (six or seven stations per fish). The anchor slipped during data collection on the first 1996 fish, a 67-cm male sockeye, so data are missing on the first three stations for that animal.

Hydroacoustic data were collected with a Hydroacoustics Technology Inc. (HTI), model 240 split-beam echo-sounder operating at 200 kHz and a 2.9 × 10° elliptical-beam transducer with a near-field range of 3.1 m. Pulses were 0.2 ms long, transmitted at a rate of 8/s in 1995 and 11/s in 1996. Echoes were rejected if they did not meet a minimum amplitude of 0.6 V, equivalent to a –35 dB target on axis. PW was measured in digital sampling units (48 000 sampling units/s) at 6, 12, and 18 dB below peak amplitude. In 1995, echoes with –6 dB PW between 7 and 14 sampling units, inclusive (0.15–0.29 ms), were retained for analysis. In 1996, acquisition criteria were liberalized to 5–19 sampling units (0.10–0.40 ms), and data were subsequently filtered to match the 1995 criteria. The system was calibrated in April of 1995 and 1996. Reciprocity calibrations with a naval standard transducer were performed and calibration results were verified using a 38.1-mm tungsten carbide sphere. Further verification was obtained in situ by measuring the same standard sphere at the Kenai River study site on 9 May and 3 August 1995 and on 10 July 1996.

We recorded data on 350–9319 (mean = 2397) echoes per fish in 1995. In 1996, we collected 262–3568 (mean = 1225) echoes per station, totaling 5560–9447 (mean = 8327) echoes per fish. Sum-channel voltage, *x*-axis position (metres left or right of the beam axis), *y*-axis position (metres up or down from the axis), range (metres from the transducer to the target), and PW at 6, 12, and 18dB below peak amplitude were measured. PW could not be measured at –12 and –18 dB for all echoes because of low signal-to-noise ratios. On average, PW was measured on 79% of echoes per fish at –12 dB and 44% at –18 dB. Beam pattern factor (correction for loss in transducer sensitivity due to location of the target off the maximum response axis) was determined from *x*–*y* coordinates using transducer calibration results. Background noise, as measured by maximum detected peak amplitude at the range of the target, ranged from 0.20 to 0.60 V, equivalent to on-axis targets with TSs from –44.5 to –35 dB.

Unrestrained fish

On 26–27 June 1996, we deployed an HTI model 240 200-kHz split-beam echo-sounder immediately above a small dam in Ship Creek in Anchorage, Alaska. Maximum water depth was 2 m and water clarity was high. Bottom substrate was silty sand. We captured 17 chinook salmon with a dip net as they moved through a gated lock in the dam, tagged them with color-coded spaghetti tags, measured them, and released them above the dam. Observers were posted, and when a tagged fish was present in the sonar beam, its identity was noted on the echogram. Hydroacoustic measurements were obtained on 10 tagged chinook salmon at ranges from 2.4 to 4.6 m from the transducer.

We used an elliptical-beam transducer with dimensions 6 × 10° and near-field range of 0.8 m. Pulses were 0.2 ms long, transmitted at a rate of 30/s. Echoes were rejected if they did not exceed a minimum amplitude of 0.39 V, equivalent to a –35 dB target on axis. Echoes with –6 dB PW between 7 and 14 sampling units, inclusive (0.15–0.29 ms), were retained for analysis. A reciprocity calibration with a naval standard transducer was performed prior to the experiment. We obtained data from 21–1378 (mean = 251, median = 71) echoes per fish.

Analytical methods

Acoustic cross section σ was estimated from each echo k using split-beam techniques (Traynor and Ehrenberg 1990). TS was estimated as

$$(1) \qquad TS = 10\log(\overline{\sigma}/4\pi)$$

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where

$$\bar{\sigma} = \frac{1}{n}\sum_{k=1}^{n}\sigma_k$$

and n was the number of valid echoes per fish.

We performed analyses of covariance to test for differences in hydroacoustic variables among species controlling for fish length and stepwise multiple linear regression analysis to find the best hydroacoustic predictors of length (Neter et al. 1990). Criteria for entering and staying in the stepwise regression model were both set to $P = 0.10$.

We calculated two indices of discriminatory power for hydroacoustic variables. First, we found the classification criterion (threshold) that maximized the average of sockeye and chinook classification success rates (proportion correctly classified) and used the maximal average success rate as the index of discriminatory power. This index had drawbacks for our application, since the consequences of classifying sockeye as chinook were more serious than those of classifying chinook as sockeye. So for a second index, we fixed the success rate for sockeye at 90%, limiting the proportion of sockeye salmon that could be misclassified as chinook salmon to 10%. The threshold was the 90th percentile of the variable of interest among the sockeye salmon sampled, and the corresponding index of discriminatory power was the chinook classification success rate.

We performed canonical discriminant analysis to find the linear combination of hydroacoustic variables that best separated sockeye salmon from chinook salmon (Fisher 1936; Johnson and Wichern 1988).

We resampled the tethered-fish data to assess the degree to which size and species discrimination would decline if hydroacoustic variables were estimated less precisely (with fewer samples) on each fish. The number of echoes per tethered fish ($\bar{n} > 2000$) far exceeded the sample sizes possible for unrestrained fish ($\bar{n} = 30 - 90$ depending on range, Burwen and Bosch 1998), which generally remain in the beam for only a few seconds. Because hydroacoustic measurements were serially correlated, we resampled by selecting a block of (30 or 90) consecutive echoes beginning at random starting points from each of the 93 tethered fish and estimated hydroacoustic parameters from those echoes alone. This process was repeated 500–1000 times, and correlation coefficients and measures of discriminatory power were averaged over all repetitions.

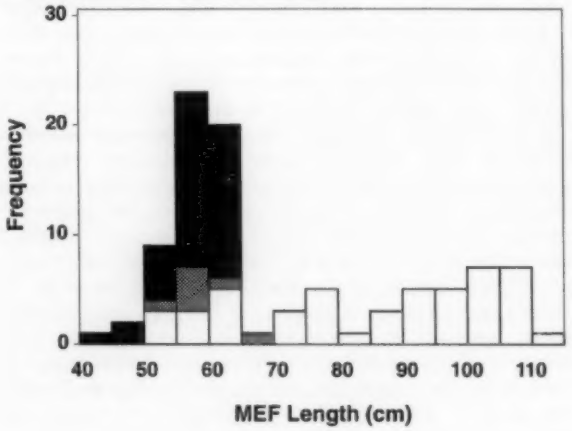
Fish exhibited different levels of activity when tethered. In particular, lateral movement (toward and away from the transducer) varied considerably and was related to fish size and species. During such movement, fish probably deviated from side aspect, and such deviations have been shown to cause large fluctuations in measured TS (Love 1977; Dahl and Mathisen 1983; Kubecka 1994; Kubecka and Duncan 1998). To quantify such movement and thereby control for its confounding effects, we calculated the absolute rate of range change between consecutive echoes as follows:

$$\text{(2)} \qquad \mathrm{RC}_k = \left|\frac{R_k - R_{k-1}}{\Delta t}\right|$$

where R_k was the range (metres from the transducer) at echo k and Δt was the time elapsed (seconds) between echoes $k - 1$ and k. We used the median range change rate of each fish as an index of its lateral movement.

We fit a series of linear statistical models (Neter et al. 1990) to quantify the effects of environmental, spatial, and behavioral factors on hydroacoustic measurements of tethered fish. Among the variables we considered for possible effects were range, tide stage, background noise, position of the fish in the beam, and lateral movement. We tested for interactions and quadratic effects and inspected residuals to verify model aptness. All models included fish length as a covariate.

Fig. 1. Frequency distribution of lengths, measured mideye to fork of tail (MEF), of 48 chinook salmon (open bars), 7 coho salmon (shaded bars), and 38 sockeye salmon (solid bars) tethered in front of a split-beam sonar.



Results

Tethered fish

Prediction of fish length

Hydroacoustic measurements were obtained on 48 chinook salmon, 38 sockeye salmon, and seven coho salmon tethered in 1995. Chinook salmon averaged 86 cm in length from mideye to fork of tail, sockeye 57 cm, and coho 59 cm (Fig. 1). Fish captured and tethered were not necessarily representative of the size and species composition at large in the Kenai River at the time of the study because we tried to obtain fish from a wide range of sizes within each species. With narrow-band sonar, hydroacoustic discrimination of species depends largely on the ability to detect differences in fish size; therefore, we first address the ability of hydroacoustic variables to predict fish length.

TS and mean PW at –6, –12, and –18 dB were all positively correlated ($P < 0.05$) with fish length, as were the standard deviations of these variables (Table 1). Mean PW was more strongly correlated with fish length than was TS. PWs measured at –12 and –18 dB were better predictors of fish size than PW at –6dB. PW variability (i.e., standard deviation) was a slightly better predictor of fish size than was mean PW. Among all variables tested, the standard deviation of –12dB PW was most strongly correlated with fish length ($r = 0.905$, $P < 0.0001$) (Table 1).

A stepwise multiple regression of fish length on TS, mean PW at –6, –12, and –18 dB (PW6, PW12, and PW18), and standard deviation of TS and PW at –6, –12, and –18 dB (TSSD, SD6, SD12, and SD18) left only SD12 and TS in the model:

$$\text{(3)} \qquad E[L] = 45.5 + 19.0\mathrm{SD12} + 0.88\mathrm{TS}$$

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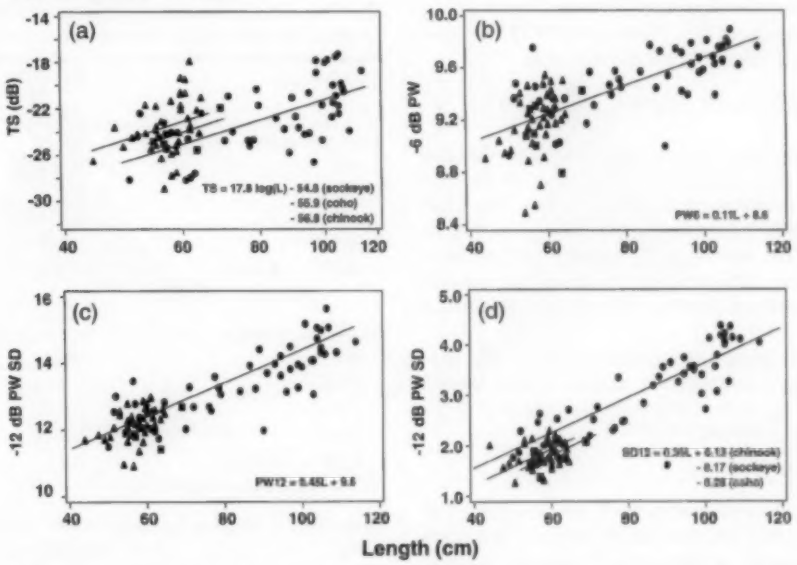
Table 1. Pearson correlation coefficients between fish length and hydroacoustic variables for 93 live Pacific salmon tethered in front of a split-beam sonar on the Kenai River.

	LEN	TS	PW6	PW12	PW18	TSSD	SD6	SD12	SD18
Length (LEN)	1.000	0.508	0.718	0.859	0.879	0.454	0.763	0.905	0.900
Target strength (TS)	0.508	1.000	0.606	0.664	0.642	0.898	0.322	0.457	0.481
–6 dB pulse width mean (PW6)	0.718	0.606	1.000	0.923	0.888	0.608	0.854	0.800	0.806
–12 dB pulse width mean (PW12)	0.859	0.664	0.923	1.000	0.992	0.623	0.827	0.926	0.922
–18 dB pulse width mean (PW18)	0.879	0.642	0.888	0.992	1.000	0.604	0.825	0.949	0.950
Target strength standard deviation (TSSD)	0.454	0.898	0.608	0.623	0.604	1.000	0.350	0.444	0.483
–6 dB pulse width standard deviation (SD6)	0.763	0.322	0.854	0.827	0.825	0.350	1.000	0.889	0.865
–12 dB pulse width standard deviation (SD12)	0.905	0.457	0.800	0.926	0.949	0.444	0.889	1.000	0.987
–18 dB pulse width standard deviation (SD18)	0.900	0.481	0.806	0.922	0.950	0.483	0.865	0.987	1.000

Note: All correlations were significantly greater than 0 at $\alpha = 0.05$.

Fig. 2. Hydroacoustic variables versus fish length for 48 chinook (circles), 7 coho (squares), and 38 sockeye salmon (triangles) tethered in front of a split-beam sonar: (*a*) target strength, (*b*) mean pulse width at –6 dB, (*c*) mean pulse width at –12 dB, and (*d*) standard deviation of pulse width at –12 dB.



where $E[L]$ is the statistical expectation of fish length. TS contributed very little prediction power to this model. Overall, the model explained $R^2 = 83\%$ of the variability in fish length, compared with $R^2 = 0.905^2 = 82\%$ for SD12 alone (Table 1). Variables SD6, SD12, and SD18 were removed from consideration for reasons later apparent. PW18 was also dropped because of its extremely high correlation with PW12 ($r = 0.992$) (Table 1) and because it was measured on fewer echoes. The multiple regression predictor of length as a function of PW12, PW6, and TS was as follows:

$$(4) \quad \begin{aligned} \text{MRF} &= E[L] \\ &= 25.7 + 26.7\text{PW12} - 33.9\text{PW6} - 0.88\text{TS} \end{aligned}$$

with $R^2 = 78\%$. For the rest of this paper, we focus on the following four hydroacoustic variables: TS, PW6, PW12, and SD12 and combinations thereof.

The linear relationship between TS and the logarithm of fish length differed among species, as did the relationship between SD12 and length ($F \geq 4.48$, df = 2,89, $P \leq 0.014$). However, chinook salmon had TS readings 2.0 dB (SE = 0.7) *lower* than sockeye salmon of the same length whereas chinook SD12 readings were about 0.31 unit (SE = 0.11) *higher* than sockeye readings (Fig. 2). The slopes of these relationships did not differ among species ($P \geq 0.21$). Neither the slopes nor the intercepts of the relationships between PW6 or PW12 and fish length differed ($P \geq 0.20$) among species.

Species discrimination

SD12 proved the best univariate discriminator between tethered sockeye and chinook salmon and TS the worst. Using SD12, one could exclude 100% of sockeye salmon while including 81% of chinook salmon or exclude 90% of sockeye salmon and include 85% of chinook salmon (Table 2). Using a TS threshold of –22.8 dB, 54% of tethered chinook salmon could be distinguished from 66% of tethered sockeye salmon, but to exclude 90% of the sockeye salmon, one would have to choose a threshold (–20.6 dB)

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Table 2. Species discrimination criteria that provided maximal average classification success for sockeye and chinook salmon and that fixed sockeye classification success at 90% for four hydroacoustic variables and one multivariate discriminant function.

	TS	PW6	PW12	SD12	CDF
Maximal average success					
Threshold value of variable	–22.81	9.34	12.99	2.31	30.48
Proportion of sockeye salmon classified correctly	0.658	0.737	1.000	1.000	0.868
Proportion of chinook salmon classified correctly	0.542	0.854	0.708	0.813	0.875
Mean proportion classified correctly	0.600	0.796	0.854	0.906	0.872
Sockeye salmon success fixed at >90%					
Threshold value of variable	–20.61	9.48	12.81	2.16	30.69
Proportion of sockeye salmon classified correctly	0.921	0.921	0.921	0.921	0.921
Proportion of chinook salmon classified correctly	0.250	0.604	0.729	0.854	0.729

Note: See Table 1 for definition of variables. Canonical discriminant function (CDF) based on three hydroacoustic variables: CDF = –0.306TS + 0.278PW6 + 1.631PW12.

that would also exclude 75% of chinook salmon. PW6 and PW12 had intermediate discriminatory power (Table 2).

The linear combination of TS, PW6, and PW12 that best discriminated sockeye from chinook salmon was

$$\text{(5)} \quad \text{CDF} = -0.306\text{TS} + 0.278\text{PW6} + 1.631\text{PW12}$$

where CDF is the canonical discriminant function. Variable SD12 was excluded from this function because of its poor performance among unrestrained fish (see below). The CDF of TS, PW6, and PW12 performed about as well as that of SD12 alone; using CDF, one could exclude 87% of sockeye salmon while including 88% of chinook salmon or exclude 90% of sockeye salmon and include 73% of chinook salmon (Table 2).

Note that the above results are germane only to this particular dataset. Actual discrimination success would depend on species composition, size distribution, sample size (echoes per fish), and other factors.

Effect of sample size

Hydroacoustic variables estimated from data resampled at 30 and 90 echoes per fish had weaker correlations with fish length and reduced power to discriminate between species. The effect of reduced sample size differed among variables (Table 3). TS was less affected than PW variables, especially PW6, which apparently had relatively high within-fish variability. However, PW12 and SD12 remained substantially better discriminators than TS at small sample sizes. At 30 echoes per fish, PW12 and SD12 could still separate 60 and 67% of tethered chinook salmon from 90% of tethered sockeye salmon whereas TS could only separate 19% of the chinook from 90% of the sockeye (Table 3). Simulated frequency distributions, by species, of selected hydroacoustic variables from the tethered-fish data resampled at 30 echoes per fish are shown in Fig. 3.

Effects of fish behavior and spatial position

Hydroacoustic measurements on tethered fish were sensitive to lateral movement by the fish and to distance from the acoustic axis (Fig. 4). In general, after controlling for fish length, fish that exhibited greater lateral movement had lower TS measurements and higher and more variable PW measurements. The following models fit the tethered fish data fairly well and explained large fractions of the variability in hydroacoustic measurements:

Table 3. Correlations with fish length, and two indices of discriminatory power, for hydroacoustic variables and functions of those variables under three different sampling rates.

	Sampling rate (echoes per fish)		
	All data[a]	n = 90	n = 30
Correlation with fish length			
TS	0.508	0.445	0.402
PW6	0.718	0.601	0.501
PW12	0.859	0.779	0.707
SD12	0.905	0.825	0.739
MRF = –8.83TS – 339PW6 + 267PW12	0.885	0.773	0.666
Maximum average classification success rate			
TS	0.600	0.560	0.553
PW6	0.796	0.712	0.671
PW12	0.854	0.780	0.749
SD12	0.906	0.824	0.787
CDF = –0.31TS + 0.28PW6 + 1.63PW12	0.871	0.791	0.745
Proportion of chinook included if 90% of sockeye excluded			
TS	0.250	0.201	0.199
PW6	0.604	0.499	0.391
PW12	0.729	0.662	0.598
SD12	0.854	0.752	0.671
CDF = –0.31TS + 0.28PW6 + 1.63PW12	0.729	0.663	0.571

Note: Data are from 93 Pacific salmon tethered in front of a split-beam sonar. MFR, multiple regression function; CDF, canonical discriminant function. See Table 1 for definition of variables.

[a]From 350 to 9319 echoes per fish, mean = 2397.

$$\text{(6)} \quad E[\text{TS}] = -49.0 + 14.4\log(L) - 13.9\text{RC} - 4.3\text{RC}\cdot\text{BPF},\ R^2 = 0.404$$

$$\text{(7)} \quad E[\text{PW6}] = 7.99 + 0.0064L + 6.7\text{RC} - 10.2\text{RC}^2,\ R^2 = 0.721$$

$$\text{(8)} \quad E[\text{PW12}] = 8.80 + 0.035L + 10.6\text{RC} - 14.3\text{RC}^2,\ R^2 = 0.791$$

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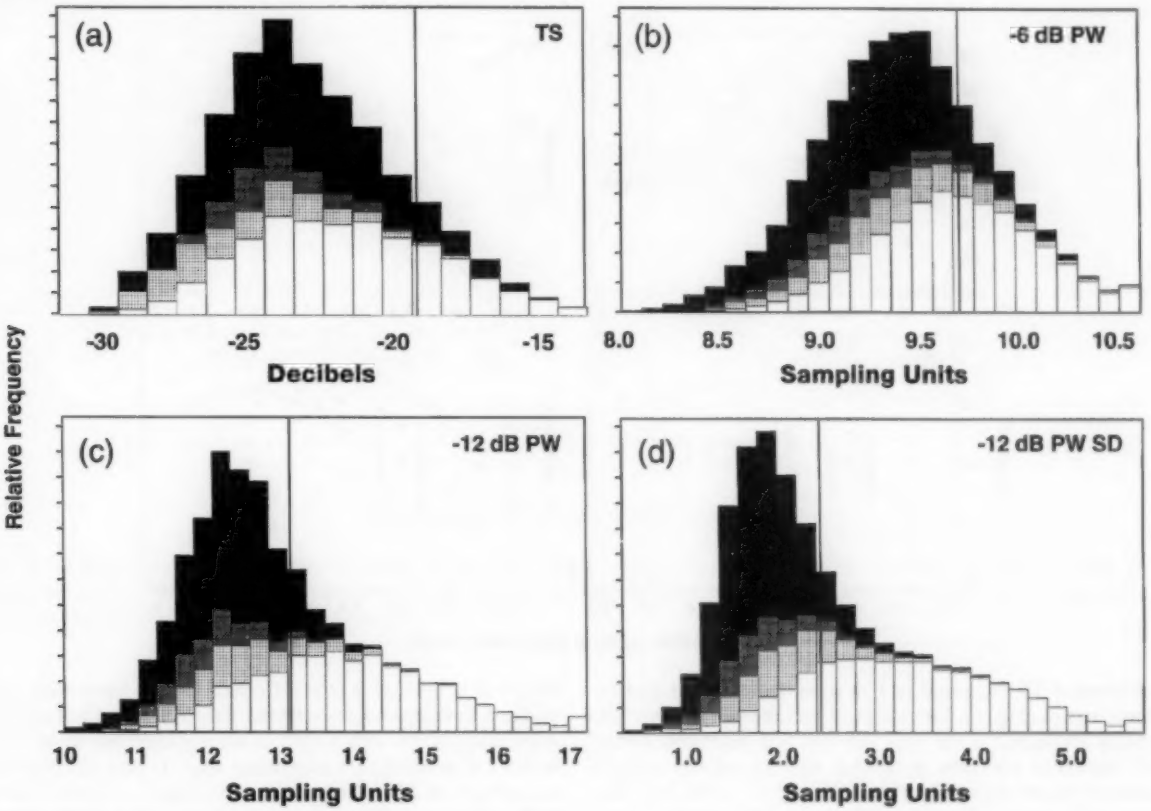
Fig. 3. Simulated frequency distributions of hydroacoustic variables measured on chinook salmon >70 cm (open bars), chinook salmon <70 cm (stippled bars), coho salmon (shaded bars), and sockeye salmon (solid bars) at 30 echoes per fish: (*a*) target strength, (*b*) mean pulse width at –6 dB, (*c*) mean pulse width at –12 dB, and (*d*) standard deviation of pulse width at –12 dB. Vertical lines represent threshold values that would exclude 90% of sockeye salmon.



(9) $E[SD12] = -0.36 + 0.028L + 3.6RC, \quad R^2 = 0.886$

where $E[\ ]$ denotes statistical expectation, L was fish length, RC was the median rate of range change (metres per second) between consecutive echoes, an index of lateral movement, and mean beam pattern factor (BPF) (decibels of lost sensitivity) was an index of the "distance" of the fish from the axis of the acoustic beam. TS declined as lateral movement increased for fish located near the maximum response axis, but lateral movement had little or no effect on TS for fish positioned off axis (Fig. 4). PW6 and PW12 increased and then declined as fish exhibited increasing lateral movement. SD12 increased linearly with lateral movement. Lateral movement itself (RC) was positively correlated with fish length ($r = 0.73$, $P < 0.0001$). Chinook salmon exhibited more lateral movement than did sockeye, even after controlling for fish length ($t = 1.98$, df = 89, $P = 0.05$).

To correct for the confounding effects of lateral movement and spatial position on hydroacoustic measurements, one can rearrange these models to define new variables. The following corrected variables have the effects of movement and position removed, thereby isolating the component of variation related to fish size:

(10) $TS_{mp} = TS + 13.9RC + 4.3RC \cdot BPF$

(11) $PW6_m = PW6 - 6.7RC + 10.2RC^2$

(12) $PW12_m = PW12 - 10.6RC + 14.3RC^2$

(13) $SD12_m = SD12 - 3.6RC.$

We interpret TS_{mp} as the estimated TS of the fish when positioned on the acoustic axis with zero lateral movement and $PW6_m$, $PW12_m$, and $SD12_m$ as estimated PW means and standard deviation under zero lateral movement.

TS corrected for movement and position (TS_{mp}) was more strongly correlated with fish length ($r = 0.63$) than was uncorrected TS ($r = 0.51$) (Table 1). Conversely, PW variables corrected for movement ($PW6_m$, $PW12_m$, and $SD12_m$) were less strongly correlated with fish length ($r = 0.63$, 0.82, and 0.88, respectively) than were their uncorrected counterparts ($r = 0.72$, 0.86, and 0.91, respectively) (Table 1).

Effect of fish orientation

Five sockeye salmon from 52 to 67 cm in length were deployed at multiple aspect angles. Although we could not determine aspect angle exactly, TS readings indicated that full side aspect was likely achieved somewhere between the first and the third stations (between 0 and 10° in Fig. 5).

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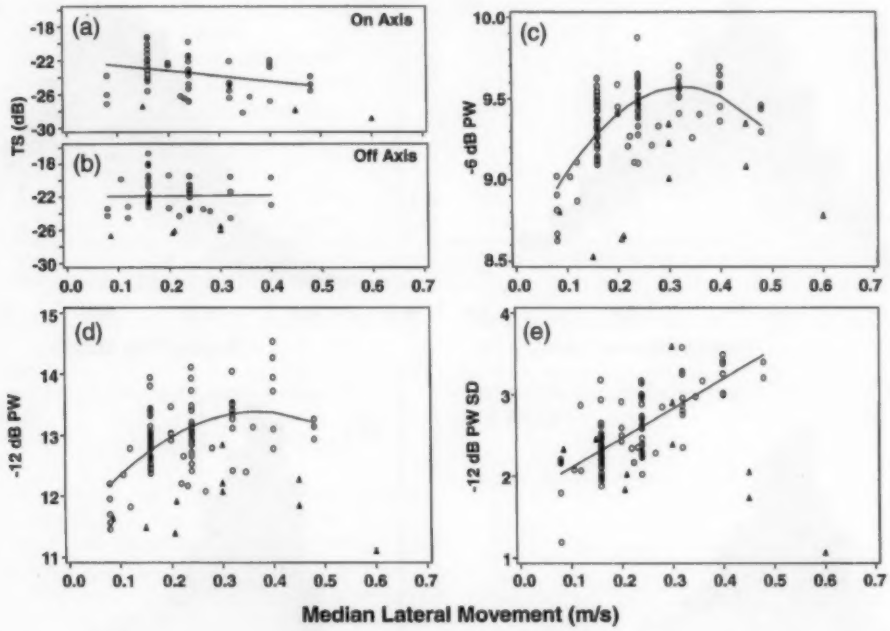
Fig. 4. Effect of lateral movement on hydroacoustic variables measured on tethered fish (circles) and unrestrained fish (triangles): (*a*) target strength measured on fish located on axis (BPF > –2.6), (*b*) target strength measured on fish located off axis (BPF < –2.6), (*c*) mean pulse width at –6 dB, (*d*) mean pulse width at –12 dB, and (*e*) standard deviation of pulse width at –12 dB. Lines are predicted values from statistical models fit to tethered fish data. Effect of fish length removed (standardized to that of a 75-cm salmon).



Estimated TS decreased as fish were ensonified at greater aspect angles (Fig. 5). The range of variation in TS over all aspects averaged 7.2 dB over the five fish deployed. Mean PW increased and then decreased with increasing aspect; maximal values occurred between 10 and 15° from full side aspect. The range of variation averaged 0.41 sampling unit for PW6 and 1.48 sampling units for PW12 over the five fish deployed. SD12 also increased and then decreased with increasing aspect angle; maximal values occurred 15–25° from full side aspect. The range of variation in SD12 averaged 1.03 sampling units over the five fish deployed (Fig. 5).

Unrestrained fish

TS of unrestrained chinook salmon in Ship Creek was positively correlated with fish length ($r = 0.67$, $P = 0.04$) as were PW6 ($r = 0.68$, $P = 0.03$) and PW12 ($r = 0.83$, $P = 0.003$). Slopes of relationships between TS, PW6, PW12, and length for unrestrained chinook salmon did not differ from those of tethered chinook salmon (F tests, $P \geq 0.12$); however, the intercepts were all significantly lower (F tests, $P < 0.0001$) (Fig. 6).

Measurements of TS, PW6, and PW12 on unrestrained chinook salmon were affected by lateral movement and spatial position in much the same manner as were measurements on tethered salmon. The effect of lateral movement on TS depended on position of the fish in the beam, and the effect of lateral movement on mean PW was again markedly nonlinear (Fig. 4). As with tethered fish, lateral movement (median range change rate) was positively related to fish length ($r = 0.65$, $P = 0.04$). Corrections for movement and position developed from tethered fish (eq. 10) improved the correlation of TS with length of unrestrained fish from 0.67 to 0.80. Corrections for movement (eqs. 11 and 12) had minor effects on PW6 (correlation with length decreased from 0.68 to 0.63) and PW12 (increased from 0.83 to 0.85). Mean PW measured on unrestrained fish was also sensitive to mean range from the transducer; PW6 and PW12 increased with range after controlling for fish length ($P \leq 0.004$).

SD12 was not significantly correlated with fish length for Ship Creek chinook salmon ($r = 0.32$, $P = 0.37$) (Fig. 6). SD12 was affected by lateral movement very differently among unrestrained chinook than among tethered salmon (Fig. 4). Whereas SD12 was linearly related to median lateral movement among tethered fish, it declined sharply among unrestrained fish when median lateral movement exceeded 0.3 m/s. After applying the correction for movement developed from tethered fish (eq. 13), the correlation of SD12 with fish length declined from 0.32 to –0.14.

Discussion

TS measurements from this study are consistent with previous work. Numerous studies have documented a linear relationship between TS and (the logarithm of) fish length (see review by McClatchie et al. 1996). In a marine setting with downward-looking sonar and dorsal-aspect measurements, the relationship can be precise, and TS can be used to discriminate, to some degree, between species greatly different in size or anatomy (Rose and Leggett 1988). In side-looking

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Fig. 5. Hydroacoustic variables plotted against relative aspect angle for five sockeye salmon tethered in front of a split-beam sonar: (*a*) target strength, (*b*) mean pulse width at –6 dB, (*c*) mean pulse width at –12 dB, and (*d*) standard deviation of pulse width at –12 dB. Fish lengths were 54 cm (circles), 59 cm (squares), 62 cm (asterisks), 63 cm (crosses), and 67 cm (diamonds).

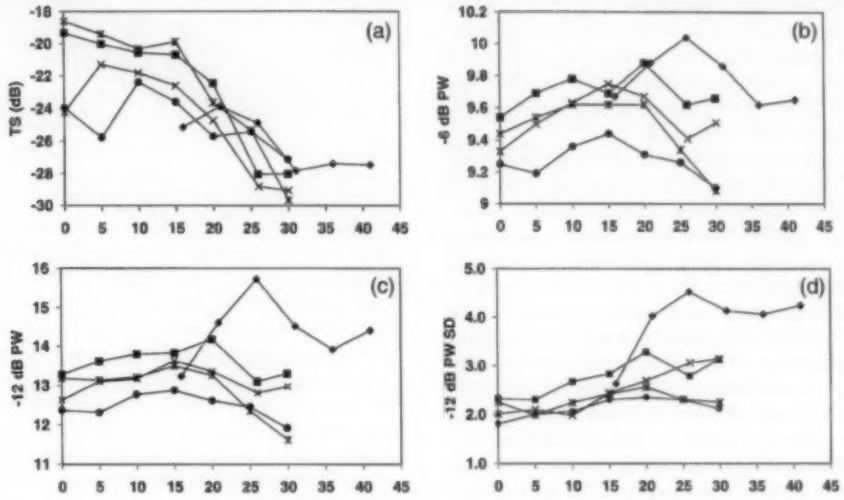
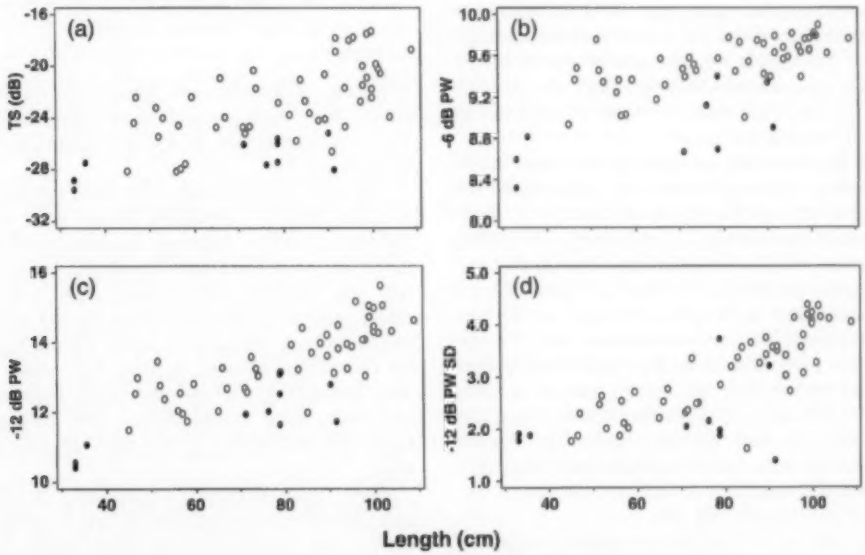


Fig. 6. Hydroacoustic variables versus fish length for 10 unrestrained chinook salmon (solid circles): (*a*) target strength, (*b*) mean pulse width at –6 dB, (*c*) mean pulse width at –12 dB, and (*d*) standard deviation of pulse width at –12 dB. Open circles represent tethered chinook salmon from Fig. 2 for comparison.



applications in rivers, however, TS measurements are more variable and discriminatory power is severely curtailed. Neither Johnston and Hopelain (1990) nor Vaught and Skvorc (1993) were able to discern modes in TS distributions that reflected those found in the underlying fish length distributions. Eggers (1994) concluded that, theoretically, within-fish TS variability alone was sufficient to obscure two distinct modes in fish length distribution, thereby making discrimination difficult and unreliable. Daum and Osborne (1996) found no significant relationship between fish length and mean TS measured on 42 chum salmon (*Oncorhynchus keta*) at an average of 33 echoes per fish. Our study found a significant relationship between TS and length, but it was very imprecise, even at more than 2000 echoes per fish. Sockeye salmon had higher TS readings than chinook salmon of the same length, which further compromised any ability to discriminate species based on TS measurements alone.

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In contrast, PW had an unexpectedly strong correlation with fish size. Moreover, PW was a far better discriminator of (tethered) fish species than was TS. To our knowledge, there has been little previous consideration of PW as a discriminatory variable. Vray et al. (1990) found that pulse duration did not aid in discriminating between lacustrine fish species with downward-looking sonar. Given our findings, further tests of PW as a species discriminator for other hydroacoustic applications are warranted.

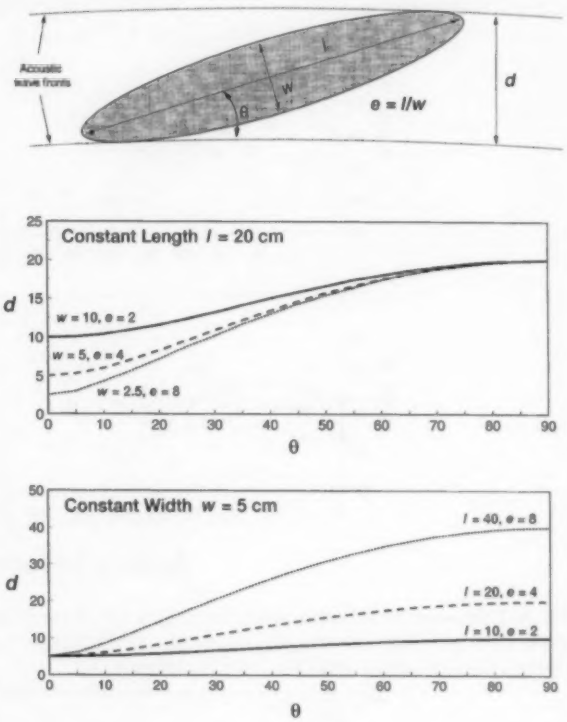
Multivariate approaches to size prediction and species discrimination were less effective than expected. The CDF yielded only a modest improvement in discriminatory power over PW12 alone, partly because positive correlations among component variables (Table 1) limited the potential for large increases in discriminatory power as new variables were added. We believe that the multivariate approach could be very effective if hydroacoustic behavioral variables (e.g., swim speed, range change rate) could be utilized as additional independent discriminators along with TS and PW. More measurements of unrestrained fish of known size and species would be required to develop such models.

Hydroacoustic measurements have high within-fish variability, so large sample sizes are desirable for species discrimination. Sample sizes obtained from tethered fish are not possible with unrestrained fish. At 30 echoes per fish, even the most promising discriminatory variables resulted in unimodal distributions (Fig. 3) despite the bimodal distribution of fish length (Fig. 1). Under these conditions, hydroacoustic measurements still contain information about fish size, but utilizing such information becomes more difficult. Without a frequency distribution that reflects the modes of the underlying fish size distribution, selecting an appropriate threshold becomes very subjective. Greater and (or) more distinct differences in fish size between species would be required to offset the effect of small sample size.

Hydroacoustic measurements on tethered fish were sensitive to fish behavior, spatial position, and orientation. TS and PW were sensitive to fish orientation in the yaw plane (aspect) and to lateral movement. Lateral movement probably influenced hydroacoustic measurements through its association with changing orientation as the fish swam left or right. The negative effect of lateral movement on TS declined for fish positioned far from the acoustic axis. We believe this interaction to be related to threshold-induced bias (more small echoes censored by the voltage threshold when the fish is off axis, Weimer and Ehrenberg 1975). Also, additive reverberative noise may disproportionately influence small-amplitude echoes from fish located off axis. Both factors would dampen the reduction in TS with increased lateral movement for fish located off axis.

Fish orientation affected TS and PW in differing ways. TS declined almost monotonically with increasing departures from side aspect, which is consistent with the results of previous experiments on anaesthetized fish (Love 1977; Dahl and Mathisen 1983; Kubecka 1994; Kubecka and Duncan 1998). TS also declined with increasing lateral movement among fish located near the center of the beam. In contrast, PW mean and standard deviation increased with moderate departures from side aspect and then declined at large aspect angles. Maximal values were achieved between 10 and 25° from full side aspect. These findings are consistent with the nonlinear dependence of mean PW on lateral movement among both tethered and unrestrained fish (Fig. 4). Mean PW was maximized at median lateral movement between 0.3 and 0.4 m/s.

Fig. 7. Geometric model of pulse elongation described in the text.



The differing responses of TS and PW to fish behavior are at least partially responsible for the large differences in discriminatory power between the two variables. In our study, large fish exhibited more lateral movement than did smaller fish and chinook salmon more than sockeye salmon. Because greater lateral movement caused *lower* TS measurements among large fish, size-related differences in TS between large chinook salmon and small sockeye salmon were diminished. On the other hand, because (moderate) lateral movement caused *higher* PW measurements among large fish, differences in PW between species were accentuated.

Given these findings, the success of hydroacoustic size and species discrimination may hinge on fish orientation, behavior, and spatial position. Under some conditions (movement positively related to fish size), behavior differences may actually enhance the discriminatory power of PW. Such conditions may not be uncommon; they were present among both tethered and unrestrained fish in this study. Discrimination success would also depend on how much these confounding factors vary over time. Temporal changes in orientation, behavior, or spatial position would introduce additional variability that could obscure any differences due to fish size or species composition. For example, TS differences due to changing aspect alone averaged 7.2 dB in this

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study, greatly exceeding differences due to fish size. Given the slope of the TS–log(length) relationship in this study (17.8), one would expect only a 3.8-dB difference in TS between a 60-cm salmon and a 100-cm salmon. TS distributions could thus be affected more by changes in migratory path or behavior over time than by real changes in fish size or species composition. PW measurements would be subject to the same problem, although to a lesser degree because of the nonmonotonic effects of orientation and behavior on PW.

To some extent, it may be feasible to reduce the sensitivity of hydroacoustic measurements to fish behavior by employing corrections similar to those demonstrated in this paper. Such corrections remove confounding effects and isolate the component of hydroacoustic information that is related to fish size. When TS was corrected to remove the effects of differential lateral movement and spatial position, its correlation with fish length increased from 0.51 to 0.63. TS corrected in this way was not only a better index of size (and a better discriminator of species), it would also be less sensitive to changes in behavior and position. Corrected PW would also be less sensitive to changes in fish behavior. Note that when PW was corrected for lateral movement, its correlation with length usually decreased somewhat due to the association between fish size and lateral movement in our studies. If fish behavior fluctuated over time, or lateral movement was not positively related to fish size, correction for behavioral effects would improve the discriminatory power of PW. Corrected variables should preferably be developed on a site-specific basis (but see below).

Measurements of unrestrained chinook salmon in Ship Creek were, for the most part, consistent with those from tethered fish in the Kenai River despite the very different conditions at the two sites. Mean PW (at least PW12) remained a better size predictor than TS. Furthermore, lateral movement and spatial position affected TS, PW6, and PW12 similarly among both tethered and unrestrained fish, suggesting that corrections based on data from one application may be portable to others. In contrast, the best predictor of size among tethered fish (SD12) was only weakly correlated with length of unrestrained fish, and the nature of the sensitivity of SD12 to lateral movement differed substantially between the two data sets. Correction of SD12 for movement eliminated all positive correlation with length. These findings are disappointing but not necessarily surprising. Given the sensitivity of PW to orientation and behavior, it seems reasonable that PW variability (e.g., SD12) might be more sensitive to differing conditions and behavior than mean PW. Clearly, our understanding of the factors that control PW variability is incomplete, and therefore, the utility of PW standard deviation as a species discriminator may be limited.

Shortcomings of our unrestrained fish data include small sample size and very short ranges (<5 m). Opportunities to obtain data like these are very limited; we were restricted to small streams with good water clarity where we could capture, mark, and observe fish. The short range at which the unrestrained fish data were collected may explain the observed dependence of mean PW on range. The acoustic beam was small relative to the length of the fish, and many echoes may have originated from only a portion of the fish's body. Mean PW did not increase with range among tethered fish deployed at ranges from 13 to 41 m.

Detailed consideration of the physical mechanisms behind the PW–length relationship is beyond the scope of this paper. However, we present the following simple geometric model, based on work by Ehrenberg and Johnston (1996), as a starting point for such a discussion. A target should scatter sound for as long as the transmitted pulse intersects any part of the target. Therefore the elongation of the backscattered pulse (over and above the length of the transmitted pulse) should be directly related to the maximum dimension of the target in the direction of the incident sound wave (Fig. 7). If the target (fish swim bladder) approximates an ellipse in cross section, then this distance can be described by

$$d = \sqrt{l^2 \sin^2 \theta + w^2 \cos^2 \theta} \quad (14)$$

where l is the length of the swim bladder, w is its width, and θ is the orientation angle (degrees of departure from full side aspect). Under this model, distance d (and therefore, pulse elongation) is dependent primarily on the width of the target at small angles θ, and the length of the target becomes more important as θ increases (Fig. 7). Furthermore, the sensitivity of PW measurements to orientation and behavior is determined by the relative elongation of the target $e = l/w$. To date, we have not been able to estimate the effective elongation of salmon as acoustic targets from our tethered fish experiments. Note that the above model predicts increases in PW with orientation angle as well as with length, as observed. However, it does not explain the observed decline in PW at large aspect angles. We speculate that this phenomenon is related to the decline in echo amplitude as orientation angle increases and that the decline in PW with angle would be less pronounced under conditions with better signal-to-noise ratios. Tank experiments with anaesthetized fish may be necessary to resolve some of these questions.

We conclude that side-aspect hydroacoustic measurements contain substantial information about fish size and that some size and species discrimination may be possible in rivers under the right conditions. Conditions that favor hydroacoustic species discrimination include large differences in size between species, large sample sizes (many echoes per fish), and consistent fish orientation and behavior. We are encouraged by the apparent association between fish size and PW but caution that behavior may play a large part in that association. It may be possible to reduce the sensitivity of hydroacoustic measurements to fish behavior by developing simple corrections based on statistical models of hydroacoustic data. More work will be necessary to test the generality of our findings.

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References

Burwen, D.L., and Bosch, D.E. 1998. Estimates of chinook salmon abundance in the Kenai River using split-beam sonar, 1996. Fish. Data Ser. No. 98-2, Alaska Department of Fish and Game, Anchorage, Alaska.

Burwen, D.L., Bosch, D.E., and Fleischman, S.J. 1998. Evaluation of hydroacoustic assessment techniques for chinook salmon on the Kenai River, 1995. Fish. Data Ser. No. 98-3, Alaska Department of Fish and Game, Anchorage, Alaska.

Dahl, P.H., and Mathisen, O.A. 1983. Measurements of fish target strength and associated directivity at high frequencies. J. Acoust. Soc. Am. **73**:1205–1211.

Daum, D.W., and Osborne, B.M. 1996. Enumeration of Chandalar River fall chum salmon using split-beam sonar, 1995. Alaska Fish. Prog. Rep. 96-2, U.S. Fish and Wildlife Service, Fishery Resource Office, Fairbanks, Alaska.

Eggers, D.M. 1994. On the discrimination of sockeye and chinook salmon in the Kenai River based on target strength determined with 420 kHz dual-beam sonar. Alaska Fish. Res. Bull. **1**(2): 125–138.

Eggers, D.M., Skvorc, P.A., II, and Burwen, D.L. 1995. Abundance estimates of chinook salmon in the Kenai River using dual-beam sonar. Alaska Fish. Res. Bull. **2**(1): 1–22.

Ehrenberg, J.E., and Johnston, S.V. 1996. Evaluation of the use of hydroacoustic pulse width data to separate fish by size group. Report prepared for Alaska Department of Fish and Game, Sport Fish Division, 333 Raspberry Rd., Anchorage AK 99518, U.S.A.

Fisher, R.A. 1936. The use of multiple measurements in taxonomic problems. Ann. Eugenics, **7**: 179–188.

Gaudet, D.M. 1990. Enumeration of migrating salmon populations using fixed-location sonar counters. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **189**: 197–209.

Johnson, R.A., and Wichern, D.W. 1988. Applied multivariate statistical analysis. Prentice-Hall, Englewood Cliffs, N.J.

Johnston, S.V., and Hopelain, J.S. 1990. The application of dual-beam target tracking and Doppler-shifted echo processing to assess upstream salmonid migration in the Klamath River, California. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **189**: 210–222.

Kubecka J., 1994. Simple model on the relationship between fish acoustical target strength and aspect for high-frequency sonar in shallow waters. J. Appl. Ichthyol. **10**: 75–81.

Kubecka, J., and Duncan, A. 1998. Acoustic size vs. real size relationships for common species of riverine fish. Fish. Res. (Amst.), **35**: 115–125.

Love, R.H. 1969. Maximum side-aspect target strength of an individual fish. J. Acoust. Soc. Am. **46**: 746–752.

Love, R.H. 1977. Target strength of an individual fish at any aspect. J. Acoust. Soc. Am. **62**: 1397–1403.

McClatchie, S., Alsop, J., and Coombs, R.F. 1996. A re-evaluation of relationships between fish size, acoustic frequency, and target strength. ICES J. Mar. Sci. **53**: 780–791.

Mesiar, D.C., Eggers, D.M., and Gaudet, D.M. 1990. Development of techniques for the application of hydroacoustics to counting migratory fish in large rivers. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **189**: 223–231.

Neter, J., Wasserman, W., and Kutner, M.H. 1990. Applied linear statistical models. Richard Irwin, Boston.

Rose, G.A., and Leggett, W.C. 1988. Hydroacoustic signal classification of fish schools by species. Can. J. Fish. Aquat. Sci. **45**: 597–604.

Traynor, J.J., and Ehrenberg, J.E. 1990. Fish and standard sphere target-strength measurements obtained with a dual-beam and split-beam echo-sounding system. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **189**: 325–334.

Vaught, K.D., and Skvorc, P.A., II. 1993. Feasibility of split-beam hydroacoustic gear to provide estimates of coho salmon abundance in the Kenai River. Regional Inf. Rep. No. 5J93-05, Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division, Juneau, Alaska.

Vray, D., Gimeniz, G., and Person, R. 1990. Attempt at classification of echo-sounder signals based on the linear discriminant function of Fisher. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **189**: 388–393.

Weimer, R.T., and Ehrenberg, J.E. 1975. Analysis of threshold-induced bias inherent in acoustic scattering cross-section estimates of individual fish. J. Fish. Res. Board Can. **32**: 2547–2551.

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Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks

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Abstract: We used a multi-stock comparison to identify spatial and temporal characteristics of environmentally driven sources of variability across four decades in the productivity of 29 sockeye salmon (*Oncorhynchus nerka*) stocks from British Columbia (B.C.) and Alaska. We examined patterns of covariation among indices of survival rate (residuals from the best-fit stock-recruitment curve) and found positive covariation among Fraser River sockeye stocks (southern B.C.) and, to a greater extent, among Bristol Bay stocks (western Alaska) but no evidence of covariation between these two regions or with stocks of other regions in B.C. and Alaska. This indicates that important environmental processes affecting variation in sockeye survival rate from spawners to recruits operate at regional spatial scales, rather than at the larger, ocean-basin scale. The observed covariation in survival rates of Bristol Bay stocks appears to be due to a combination of both freshwater and, to a greater degree, marine processes. Bristol Bay sockeye stocks showed a dramatic and persistent increase in survival rates coinciding with the abrupt changes in the North Pacific environment in the mid-1970s; however, there was little evidence of a similar response for Fraser River stocks.

Résumé : Nous avons utilisé une comparaison multi-stocks pour établir les caractéristiques spatiales et temporelles des sources environnementales de variabilité sur quatre décennies dans la productivité de 29 stocks de saumon rouge (*Oncorhynchus nerka*) de la Colombie-Britannique (C.-B.) et de l'Alaska. Nous avons examiné les profils de covariation entre des indices du taux de survie (résidus de la courbe stock-recrutement de meilleur ajustement) et trouvé qu'il existe une covariation parmi les stocks de saumon rouge du Fraser (sud de la C.-B.), et une covariation encore plus marquée parmi les stocks de la baie Bristol (ouest de l'Alaska), mais qu'il n'y a pas de covariation entre ces deux régions ou avec les stocks d'autres régions de la C.-B. et de l'Alaska. Cela montre que d'importants processus environnementaux qui font varier le taux de survie du saumon rouge des reproducteurs jusqu'aux recrues agissent à des échelles spatiales régionales plutôt qu'à l'échelle élargie du bassin océanique. La covariation observée des taux de survie des stocks de la baie Bristol semble être due à une combinaison de processus dulcicoles mais surtout marins. Les stocks de saumon rouge de la baie Bristol ont connu un accroissement marqué et persistant du taux de survie qui a coïncidé avec les changements abrupts survenus dans l'environnement du Pacifique Nord au milieu des années 70; cependant, on dispose de peu d'indices montrant que les stocks du Fraser auraient réagi de façon similaire.

[Traduit par la Rédaction]

Introduction

Year-to-year variation in recruitment of Pacific salmon (*Oncorhynchus* spp.) has practical implications. Despite extensive adjustments to harvesting regulations during each fishing season (e.g., Minard and Meacham 1987), unusually large recruitments tend to lead to over-escapements (more fish on spawning grounds than desired), and unusually small recruitments tend to lead to under-escapements (Bocking and Peterman 1988). Variability in recruitment thus creates risks, not only for fish stocks, but also for management agencies and industry (in terms of foregone yield and capital investment decisions that are based on expected future returns from salmon stocks). Furthermore, variation makes it difficult to interpret effects of past management strategies (such as harvest policies or enhancement programs) and therefore leads to uncertainties about underlying biological relationships and about best choices for future management strategies.

For Pacific salmon, the biomass of recruits available to be harvested is influenced by variation in three component processes: survival rate from eggs to adult recruits (referred to here as productivity), somatic growth rate, and age-at-maturity schedule. Salmon recruitment data are characterized by large variation in survival rates among years and smaller temporal variation in growth rates and mean age at

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maturity. Stock-recruitment relationships usually explain little of the variation in survival rates, which suggests that environmental processes are important (Peterman 1987). Indeed, many single-stock studies have developed hypotheses and supporting evidence for the influence of various environmental processes in freshwater, estuarine, or marine life stages on components of salmon recruitment (for reviews, see Pearcy (1992), Beamish (1995), and Emmett and Schiewe (1997)). However, as Walters and Collie (1988) indicated, caution must be used when interpreting single-stock cases. Such relationships often break down over time as new data are gathered, suggesting that many of the observed correlations may have been spurious. A more powerful method to generate and test hypotheses about environmental effects on fish is to determine whether there are similar patterns of temporal variation in recruitment processes among stocks of the same or similar species that utilize overlapping or nearby areas. Covariation can suggest hypotheses about sources of environmentally driven variability that reflect the geographic area and particular life stage(s) where these stocks experience similar environmental conditions. Multi-stock analyses have been found useful, to varying degrees, by Thompson and Page (1989), Koslow et al. (1987), Ware and McFarlane (1989), Myers et al. (1997), and Adkison et al. (1996).

The objective of our research was to use this multi-stock approach to develop a better understanding of the spatial and temporal characteristics of environmental (physical and biological) processes that affect the three components of recruitment biomass of sockeye salmon (*O. nerka*). This paper focuses only on survival rates. A second paper (B. Pyper, R.M. Peterman, M.F. Lapointe, and C.J. Walters, School of Resource and Environmental Management, Simon Fraser University, Burnaby, B.C., unpublished data) examines growth rate and age at maturity and compares patterns of covariation among these components and survival rate.

We investigated patterns of covariation in survival rate for sockeye salmon stocks from various regions in the Northeastern Pacific — western, central, and southeastern Alaska and north-central and southern British Columbia (B.C.). We focused on sockeye salmon stocks because a large number of these stocks have data covering roughly 40 years. Furthermore, high-seas tagging and freshwater recovery data (French et al. 1976) show that sockeye stocks from Alaska and B.C. overlap in space and time in the Gulf of Alaska for 1 to 2 years after they migrate away from coastal regions as juveniles and before they return as adults to natal streams to spawn. During this period of overlap, stocks are in what Ware and McFarlane (1989) called the Central Subarctic Domain of production, where different stocks may be subjected to similar influences of oceanographic conditions (temperature, upwelling, and current patterns) that likely affect food supply and predators. The areas where distributions of Alaskan and B.C. sockeye stocks are separate include their freshwater habitats and coastal marine regions through which juveniles and returning adults must pass.

The degree to which certain stocks share common conditions will determine the strengths and patterns of covariation in survival rate observed. In this study, we compared patterns of covariation in indices of survival rates at two spatial scales: (*i*) across stocks from different regions (reflecting large-scale or "ocean-basin" processes that affect all stocks from western Alaska to southern British Columbia) and (*ii*) across stocks within a region (reflecting regional-scale processes, e.g., across stocks having smolts that migrate into Bristol Bay, Alaska).

Our research is based on a uniquely large data set and differs from other investigations of environmental variability in sockeye salmon stocks in four ways: (*i*) the number of different sockeye salmon stocks analysed (29); (*ii*) the long time span (24 to 45 years); (*iii*) the wide geographical range of spawning areas (river mouths separated by over 2400 km between western Alaska and southern B.C.); and (*iv*) in addition, we used a survival rate index that accounted for the effect of interannual variability in spawner abundance on survival rate (see Methods). This survival-rate index was similar to the one used by Walters and Staley (1987) and Collie et al. (1990) but differs from simple indices of productivity such as catch or abundance of recruits used by many other studies (e.g., Beamish and Bouillon 1993; Hare and Francis 1995; Mantua et al. 1997). Catch or recruitment indices of productivity may be confounded by changes in spawner abundance, which could distort or mask the signal of environmental effects on salmon productivity. This paper extends the previous work of Adkison et al. (1996) by adding recent years of data, nine stocks from regions located between Bristol Bay and Fraser River, and separate data on survival rates in freshwater and marine life stages.

Methods

Data

Spawners and recruits

We used age-specific abundance data for spawners and recruits (catch plus escapement) for the following sockeye salmon stocks. For Alaska, we analyzed data for 9 Bristol Bay stocks (Branch, Egegik, Igushik, Kvichak, Naknek, Nuyakuk, Togiak, Ugashik, and Wood) for brood years (year of spawning) 1956 through 1991 (Bev Cross, Alaska Department of Fish and Game, Anchorage, Alaska, personal communication), the Upper Cook Inlet stock complex for brood years 1968 through 1991 (David Waltemyer, Alaska Department of Fish and Game, Soldotna, Alaska, personal communication), and the Copper River stock complex for brood years 1961 through 1991 (John Wilcock, Alaska Department of Fish and Game, Cordova, Alaska, personal communication). The B.C. sockeye data covered the Nass River stock for brood years 1967 through 1991 (L. Jantz, Canadian Department of Fisheries and Oceans, Prince George, B.C., personal communication), the Skeena River stock for brood years 1948 through 1992 (L. Jantz, personal communication), and 16 Fraser River stocks (Adams, Birkenhead, Bowron, Chilko, Cultus, Early Stuart, Gates, Horsefly, Late Stuart, Nadina, Pitt, Portage, Raft, Seymour, Stellako, and Weaver) for brood years 1948 through 1992 (Jim Woodey, Pacific Salmon Commission, Vancouver, B.C., personal communication). For the Chilko stock, only data up to brood year 1988 were used because lake fertilization began after that.

We used the best available measure of spawning potential for each stock to compute indices of survival rate. For all Alaskan stocks and for the Nass stock, total numbers of spawners were used. For the Skeena stock, total numbers of adult spawners were used (i.e., jacks, or precocious male spawners, were excluded because these fish often represented a large proportion of the spawners). For all Fraser River stocks except Cultus, we used the number of "effective" female spawners as the measure of spawner abundance. This was the number of female spawners in a given year

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multiplied by the average proportion of eggs laid (as opposed to retained in the body) in that year (estimated by spawning-ground surveys). Total numbers of female spawners were used for the Cultus stock because such egg-retention data were not available. Although abundance data were available for a few other stocks of Fraser River sockeye salmon, we used only those stocks that had 20 or more years of data with at least 500 "effective" female spawners.

Smolt abundance

We used abundances of age-1 and age-2 smolts (i.e., those that overwintered in a rearing lake for one or two winters, respectively) for the following brood years and stocks: Chilko sockeye (1949 through 1988; J. Woodey, personal communication), age-1 smolts for Skeena sockeye (1959 through 1994; L. Jantz, personal communication), and age-1 and age-2 smolts estimated by acoustic methods for four Bristol Bay sockeye stocks (B. Cross, personal communication): Egegik (1979 through 1994), Kvichak (1968 through 1994), Ugashik (1980 through 1994), and Wood River (1972 through 1988). Smolt data for the Naknek stock were not used because only 7 brood years of data were available.

Indices of survival rate

For each stock, we calculated an index of survival rate that normalized the data and removed possible within-stock density-dependent effects. This index, referred to here as the spawner-to-recruit (SR) index, was the time series of brood-year residuals (i.e., anomalies) from a Ricker stock-recruitment model. Specifically, we used the available data for each stock to fit a Ricker model by linear regression of $\log_e$(recruits per spawner) on spawner abundance (Ricker 1975) and then calculated each brood year's SR value as the deviation from that line.

In an analogous manner, we calculated two additional indices of survival rate for each of the six stocks with smolt abundance data. First was a freshwater survival-rate index, which was the time series of residuals from the linear regression of $\log_e$(smolts per spawner) on spawner abundance, which removed possible density-dependent effects of spawner abundance on freshwater survival rate (e.g., Hume et al. 1996). Second was a marine survival-rate index, the time series of residuals from the linear regression of $\log_e$(recruits per smolt) on smolt abundance, which removed possible density-dependent effects of smolt abundance on marine survival rate (e.g., Peterman 1982). The term "marine survival rate" is commonly used in the literature, but readers should keep in mind that because smolt abundances are estimated at some convenient location in fresh water, it is possible that some of the variability in "marine survival rate" occurs during the relatively short periods when fish migrate through fresh water to reach the ocean, in estuaries, or in fresh water on their way back upstream as adults. Indices of freshwater survival rate were calculated using total smolt abundances produced for each brood year (i.e., age-1 and age-2 smolts combined where applicable). Marine indices were calculated separately for age-1 and age-2 smolts and their corresponding adult recruits (identifiable from adult scales) for the Kvichak, Egegik, Ugashik, and Wood stocks. We did not calculate a marine index for age-2 smolts of the Chilko stock because they constituted only 3% of the smolts.

Statistical analysis

Accounting for autocorrelation

Several of the time series of survival-rate indices showed positive autocorrelation typical of first-order autoregressive (AR(1)) processes, which has important implications for testing correlations between survival rates of different stocks. In general, because autocorrelated time series do not meet the assumption of independence required by the standard significance test of a correlation coefficient, such tests will have a greater Type I error rate than the specified alpha (Jenkins and Watts 1968). We therefore based our significance tests of correlation coefficients (at $\alpha = 0.05$) on an adjusted degrees of freedom, $N^* - 2$, where

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N}\sum_{j=1}^{N/5} r_{XX}(j)\,r_{YY}(j)$$

and where N was the number of sample pairs and $r_{XX}(j)$ and $r_{YY}(j)$ denote the sample autocorrelations at lag j of the two time series being correlated. Simulation analyses (Pyper and Peterman 1998) show that this test procedure, which is a modified version of the method of Chelton (1984), performs well at maintaining Type I error rates at the specified alpha when time-series data contain positive autocorrelation typical of AR(1) processes. For most comparisons that we examined, values of adjusted degrees of freedom ($N^* - 2$) were only slightly less than the standard value (i.e., $N - 2$). An exception was for comparisons among the nine SR indices of Bristol Bay stocks, which were often moderately autocorrelated, where the average value for $N^* - 2$ was 23 compared with 32 for $N - 2$.

Combining groups of time series data

As we show later, there is evidence of positive covariation among the SR indices of Bristol Bay sockeye stocks and among Fraser River stocks. Therefore, to facilitate further analyses and presentations of results, we combined certain time series of stock-specific SR indices by averaging them into a single index for each region. This was done by first standardizing each stock-specific SR index to have unit variance (so that each index had equal weighting) and then averaging those indices across the relevant group of stocks for each year. We refer to these combined time series as "aggregated indices." Such aggregated indices have the advantage of better depicting any "signal" or variation in survival rate that is common to a group of stocks (Thompson and Page 1989) by "averaging out" stock-specific variability and measurement error.

Patterns of covariation

If shared environmental processes affect survival rates of groups of sockeye salmon stocks during either their freshwater and (or) marine life stage, then survival rates over the entire life span (our SR index) may tend to be positively correlated among those stocks. The relative magnitude of covariation should reflect the degree of similarity in physical and biological factors affecting those stocks.

To determine whether covariation exists at either the large ocean-basin or regional scale, we calculated Pearson product-moment correlation coefficients for pairwise comparisons among the spawner-to-recruit (SR) indices of survival rate for the 9 Bristol Bay stocks, the Copper, Cook, Nass, and Skeena stocks, and the 16 Fraser River stocks, giving a total of 406 (i.e., $(N^2 - N)/2$) comparisons. Data series were aligned to have brood years in common and each pairwise correlation was calculated using those years that each pair of data series had in common. To simplify presentation of results, we report average correlations for some groups of comparisons, where averages were calculated using the Fisher z-transformation of each correlation coefficient to normalize them (Zar 1984).

To examine how survival rates of a given life stage covary within or between regions, we correlated freshwater survival-rate indices among all stocks that had smolt data and repeated this procedure for their marine survival-rate indices. Freshwater indices were aligned by brood year, while marine indices of age-1 and age-2 smolts were aligned by brood year in one analysis and by a common ocean-entry year (OEY) in another. The latter approach recognizes that different age classes of smolts with the same ocean-entry year are more likely to share common marine conditions than fish with only the same brood year.

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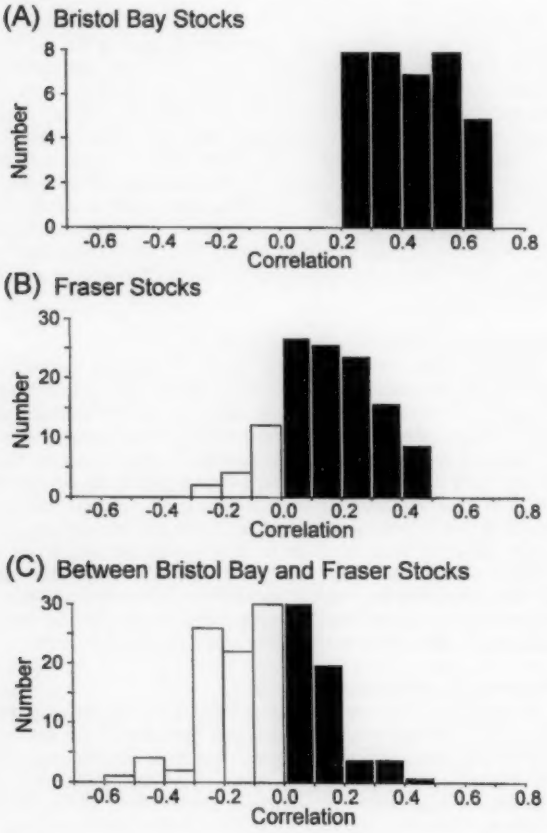
Fig. 1. Frequency distributions of correlations among the spawner-to-recruit (SR) indices of survival rate for comparisons (A) among Bristol Bay sockeye stocks, (B) among Fraser River sockeye stocks, and (C) between Bristol Bay and Fraser River stocks. Actual pairwise correlations are shown in Table 1. Open bars indicate negative correlations; solid bars are positive correlations.



Causes of patterns of covariation: freshwater or marine processes?

We also used three approaches to examine the life stage(s) at which covariation in SR indices might arise. First, we compared the magnitudes of correlations among freshwater survival-rate indices to those among marine indices for Bristol Bay stocks. Second, we examined the relative importance of freshwater and marine life stages to the variability in a given stock's SR index by correlating each of these life stage specific indices with that stock's SR index. Third, we correlated the SR, freshwater, and marine indices of a given stock with the aggregated SR index computed across all other stocks in the same region. For this third approach, we reasoned that if the positive covariation observed among SR indices was due to a particular life stage, then we would expect a high correlation between the survival-rate index of that life stage for a stock and the aggregated SR index for that region. Note that for the second and third approaches, a single marine survival-rate index was computed for each stock using the combination of age-1 and age-2 smolts of the same brood year to make appropriate comparisons with SR indices (which were computed using the total recruits by brood year, i.e., recruits from both age-1 and age-2 smolts).

Results and discussion

Patterns of covariation

The 9 Bristol Bay sockeye stocks showed strong positive covariation in SR indices of survival rate (mean correlation = 0.44, Fig. 1A). The 16 Fraser River sockeye stocks also showed a tendency toward positive covariation in SR indices, although they tended to be weaker than in Bristol Bay (mean correlation = 0.16, Fig. 1B). However, there was no general tendency for Bristol Bay SR indices to be correlated with those of Fraser River stocks (mean correlation = –0.05; Fig. 1C).

All 36 correlations (r values) among Bristol Bay stocks were positive (signs test, $P < 0.001$) and 21 of these were significant ($P < 0.05$; Table 1), many more than the one significant positive case expected on average by chance alone at $\alpha = 0.05$ if there were no correlation. To put the magnitude of these correlations among Bristol Bay SR indices into perspective, suppose that survival rates at the freshwater and marine life stages of a given stock are independent and account for similar proportions of variability, as Bradford's (1995) analysis of data for sockeye salmon suggests. Then, if survival rates in one of these life stages covaried perfectly among stocks (i.e., $r = 1$), while the other was independent among stocks (i.e., $r = 0$), the correlation expected between two stocks' overall SR indices would be only 0.5. This corresponds to a proportion of common variance of just 25% (i.e., $r^2 \times 100$), even though 100% of the variance in survival rate was shared for one of the life stages. In other words, independent variability among stocks in a given life stage will tend to profoundly mask covariation among stocks in another life stage. Moreover, the widely recognized random measurement error in estimates of spawner and recruit abundances will reduce correlations even further. For these reasons, we view the average correlation of 0.44 among Bristol Bay SR indices as strong evidence of important common environmental processes influencing one or more life stages of these stocks.

Correlations among Fraser River SR indices consisted of 102 positive r values out of the 120 correlations calculated (signs test, $P < 0.001$), showing a strong tendency toward positive covariation in survival rates. Twenty-five correlations among Fraser stocks were significant ($P < 0.05$; Table 1), and all of these were positive, many more than the three expected on average by chance alone at $\alpha = 0.05$. It is possible that we have overestimated the degree of covariation in survival rate among Fraser stocks as the result of imperfect stock identification in catch data, which would lead to some fish of an abundant stock being misallocated to smaller stocks that share a similar run timing (Cass and Wood 1994). However, for the eight most abundant Fraser stocks, which fall into four distinct run-timing groups (Early Stuart, which returns before all other Fraser stocks; Seymour, an early-summer run; Chilko, Horsefly, Late Stuart, and Stellako, mid-summer runs; and Adams and Birkenhead, late-summer runs), the average correlation among their SR indices was 0.21. Of these 28 correlations, 26 were positive, 9 of which were significant ($P < 0.05$), and only one of these significant correlations involved stocks with similar run timings (Adams and Birkenhead; Table 1). These results sug-

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Table 1. Pairwise correlation coefficients among the spawner-to-recruit (SR) indices of survival rate for sockeye salmon stocks from Alaska (Bristol Bay, Cook, and Copper) and British Columbia (Nass, Skeena, and Fraser River). Correlations significant at 0.05 are shaded.

	Branch	Egegik	Igushik	Kvichak	Naknek	Nuyakuk	Togiak	Ugashik	Wood	Cook	Copper	Nass	Skeena	Adams	Birken	Bowron	Chilko	Cultus	E. Stuart	Gates	Horsefly	L. Stuart	Nadina	Pitt	Portage	Raft	Seymour	Stellako	Weaver
Branch	--																												
Egegik	0.30	--																											
Igushik	0.68	0.21	--																										
Kvichak	0.54	0.26	0.62	--																									
Naknek	0.31	0.46	0.28	0.35	--																								
Nuyakuk	0.58	0.26	0.42	0.27	0.40	--																							
Togiak	0.38	0.36	0.27	0.33	0.30	0.42	--																						
Ugashik	0.57	0.67	0.42	0.34	0.40	0.40	0.52	--																					
Wood	0.58	0.28	0.57	0.46	0.51	0.66	0.63	0.54	--																				
Cook	-0.14	0.20	-0.21	-0.05	-0.04	-0.20	-0.05	0.18	-0.13	--																			
Copper	0.19	0.33	0.08	-0.11	0.15	-0.03	0.13	0.37	0.23	0.05	--																		
Nass	0.33	0.12	0.30	-0.07	-0.14	0.30	0.13	0.17	0.19	-0.33	0.45	--																	
Skeena	-0.00	0.30	0.18	-0.29	-0.02	-0.00	0.02	0.19	-0.02	0.09	0.24	0.40	--																
Adams	0.11	0.03	0.32	0.43	0.02	-0.05	0.12	-0.11	0.10	-0.01	-0.17	-0.02	0.09	--															
Birken	-0.05	0.22	-0.11	0.04	0.13	-0.02	-0.02	-0.07	0.07	-0.11	-0.01	-0.11	0.01	0.34	--														
Bowron	-0.26	-0.38	-0.09	-0.28	-0.15	-0.09	-0.28	-0.29	-0.28	0.11	-0.12	-0.28	0.15	0.02	-0.09	--													
Chilko	0.21	0.07	0.32	-0.08	-0.11	0.17	-0.01	0.04	0.05	-0.15	0.12	0.30	0.25	0.13	0.18	0.21	--												
Cultus	0.18	-0.03	0.17	0.10	-0.04	0.06	-0.04	0.02	0.08	-0.19	0.14	0.06	-0.02	0.30	0.09	0.37	0.14	--											
E. Stuart	-0.26	-0.28	-0.16	-0.04	-0.27	-0.23	-0.29	-0.60	-0.43	-0.11	-0.31	-0.02	0.04	0.45	0.41	0.32	-0.05	0.23	--										
Gates	-0.08	-0.04	-0.08	-0.05	0.15	0.34	-0.05	0.03	0.11	-0.23	-0.22	-0.18	-0.01	0.11	0.12	0.04	0.05	0.02	0.02	--									
Horsefly	0.05	0.15	0.04	0.24	0.18	0.19	-0.22	-0.03	-0.15	0.25	-0.17	-0.38	-0.09	0.17	0.22	0.29	0.23	0.16	0.19	-0.04	--								
L. Stuart	0.02	0.25	-0.00	-0.23	-0.06	0.08	0.08	0.06	-0.21	-0.23	-0.05	0.28	0.14	0.04	0.06	0.23	0.27	0.17	0.20	0.09	0.13	--							
Nadina	0.15	-0.21	-0.23	-0.07	-0.25	0.13	-0.02	-0.13	-0.27	0.08	-0.01	0.16	-0.03	-0.19	-0.29	0.29	0.02	0.02	0.18	-0.07	0.02	0.20	--						
Pitt	-0.28	-0.50	-0.14	0.05	-0.19	0.10	-0.26	-0.41	-0.20	-0.12	-0.41	-0.37	-0.29	0.06	0.01	0.42	-0.02	0.02	0.34	0.32	0.08	-0.02	0.19	--					
Portage	-0.11	-0.04	0.06	0.18	0.08	0.13	-0.29	-0.09	-0.11	0.06	-0.14	-0.12	0.02	0.25	0.34	-0.05	0.12	0.03	0.08	0.45	0.18	-0.04	-0.18	0.32	--				
Raft	-0.31	-0.15	-0.17	-0.42	-0.27	0.06	-0.18	-0.11	-0.28	-0.21	0.10	0.10	0.16	-0.17	-0.28	0.50	0.13	0.36	0.11	0.19	0.06	0.34	0.16	0.30	0.04	--			
Seymour	0.04	-0.05	-0.02	0.00	0.06	0.37	0.14	-0.11	0.04	0.15	-0.20	-0.31	0.06	0.43	0.34	0.27	0.40	0.30	0.30	0.26	0.38	0.07	-0.04	0.15	0.35	0.11	--		
Stellako	-0.09	0.08	0.13	-0.10	-0.26	0.18	-0.19	0.08	-0.15	0.12	-0.04	-0.09	0.41	0.02	-0.02	0.41	0.18	0.37	0.12	0.04	0.30	0.09	-0.04	0.20	0.11	0.35	0.30	--	
Weaver	-0.17	-0.21	0.02	-0.10	-0.23	0.16	-0.15	-0.21	-0.08	-0.01	-0.15	-0.15	0.13	0.24	0.08	0.27	0.09	0.21	0.07	0.26	0.19	-0.02	-0.18	0.25	0.40	0.31	0.27	0.29	--

Bristol Bay Stocks **Fraser River Stocks**

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Table 2. (A) Correlations among the freshwater survival-rate indices of the six stocks that had smolt data (top right triangle) and (B) correlations among the marine survival-rate indices of age-1 and age-2 smolts aligned to have common ocean-entry year (top right triangle).

(A) Freshwater survival-rate indices

	Egegik	Kvichak	Ugashik	Wood	Skeena	Chilko
Egegik	—	–0.37	0.46	0.25	0.39	–0.02
Kvichak	15	—	–0.53	0.36	–0.29	0.03
Ugashik	12	12	—	0.33	0.75*	0.27
Wood	9	15	8	—	–0.17	0.40
Skeena	14	23	11	15	—	–0.10
Chilko	9	18	8	16	29	—

(B) Marine survival-rate indices

	Egegik 1	Egegik 2	Kvichak 1	Kvichak 2	Ugashik 1	Ugashik 2	Wood 1	Wood 2	Skeena 1	Chilko 1
Egegik 1	—	0.12	0.32	0.10	0.66*	0.41	0.60	0.40	0.05	–0.02
Egegik 2	13	—	0.50	0.88*	0.47	0.37	0.22	–0.20	0.27	0.79*
Kvichak 1	13	13	—	0.58*	0.72*	0.11	0.80*	0.08	–0.21	0.09
Kvichak 2	13	13	23	—	0.46	0.20	0.10	–0.28	–0.10	0.40
Ugashik 1	11	11	11	11	—	0.57	0.54	–0.46	–0.30	0.21
Ugashik 2	11	11	11	11	11	—	0.02	–0.33	0.18	0.24
Wood 1	9	9	15	15	8	8	—	0.49	–0.24	0.18
Wood 2	9	9	15	15	8	8	16	—	0.07	0.00
Skeena 1	12	12	22	22	10	10	15	15	—	0.03
Chilko 1	9	9	19	19	8	8	19	19	29	—

Note: Sample sizes (in years) are shown in the bottom left triangle of both A and B. * denotes correlations that are significant ($P < 0.05$).

gest that real, although weak, positive covariation exists among survival rates of Fraser River sockeye stocks.

In contrast to these results for correlations of SR indices within regions, comparisons between stocks of different regions showed no consistent tendency toward positive or negative covariation. For example, only 59 of the 144 correlations (i.e., 41%) between Bristol Bay and Fraser River stocks were positive, and only 5 of the 144 correlations were significant ($P < 0.05$), all of which were negative (Table 1). Furthermore, there were no obvious trends toward positive or negative correlations between the SR indices of Bristol Bay or Fraser River stocks and those of the Cook, Copper, Nass, and Skeena stocks (Table 1). In fact, of these 100 correlations, there was only one significant r value ($r = 0.41$ between Skeena and Stellako). Among the Cook, Copper, Nass, and Skeena SR indices, the only significant correlation was between the Nass and Skeena stocks ($r = 0.40$), possibly because their smolts enter marine waters only 60 km apart.

Although covariation was not observed among the SR indices of stocks from *different* regions, it is possible that covariation could exist between regions in survival rates of a given life stage (e.g., marine) but be masked by independent variability in the other life stage (e.g., freshwater). However, there was little evidence of strong covariation in marine survival rates among those stocks of different regions for which we had smolt data, and the same was true for freshwater survival rates. For example, there were only non-significant correlations among the freshwater survival-rate indices of the Chilko stock (the only Fraser sockeye stock that had smolt data), the Skeena stock, and those of the Bristol Bay stocks with long time series (i.e., Kvichak and Wood; Table 2A). The same was true for the marine survival-rate indices for these stocks (Table 2B). However, it is difficult to draw any firm conclusions given the limited number of stocks and years for which freshwater and marine indices were available.

Our results on patterns of covariation show that, over the approximately 40-year period examined, variation in sockeye salmon survival rates from spawners to recruits was influenced most strongly by regional-scale environmental processes (i.e., within Bristol Bay stocks or within Fraser River stocks). In contrast, there is little evidence that environmental processes operating on an ocean-basin scale across the entire northeastern Pacific jointly affected survival rates of sockeye salmon from different regions (i.e., Alaska and B.C.). This conclusion about the greater importance of regional-scale environmental processes is consistent with findings of Myers et al. (1997) for sockeye salmon and numerous other species.

Causes of patterns of covariation: freshwater or marine processes?

The patterns of positive covariation in SR indices within regions could be due to regional covariation in freshwater survival rates, marine survival rates, or both. For instance, regional-scale weather patterns can affect freshwater flows, turbidity, and nutrients, which may lead to similar changes in productivity of freshwater life stages for stocks within a region. This situation is perhaps more plausible in Bristol Bay than for Fraser stocks because spawning areas and rearing lakes for different Bristol Bay sockeye stocks are quite similar (Burgner 1991). Furthermore, D. Rogers (Fisheries Research Institute, University of Washington, Seattle, personal communication) suggested that a common effect on the freshwater productivity of rearing lakes of Bristol Bay sockeye stocks could arise from the link between wide-

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spread increased air temperatures and increased duration of ice-free periods (and length of growing season for plankton). Similarly, it would not be surprising if there was covariation in marine survival rates of stocks within a region, which would most likely arise during early marine life when most smolt mortality is thought to occur (Ricker 1976) and when smolts from a given region share a habitat that is different from that of other regions. For instance, sockeye smolts of Fraser River stocks share similar timing, location, migration patterns, and environmental conditions that contrast greatly with those shared by migrating smolts of Bristol Bay stocks (Straty 1974; Groot and Cooke 1987). Regional-scale weather conditions (e.g., winds) may produce changes in coastal oceanographic conditions that affect food supply and distribution of predators for all stocks within a region.

Therefore, we examined three lines of evidence to assess the relative importance of freshwater and marine processes in driving covariation among SR indices within regions. As described below, our analyses suggest that the marine life stage was the more dominant source of covariation for both Bristol Bay and Fraser River stocks; however, it was again difficult to reach any firm conclusions because of the low power caused by lack of extensive smolt data.

The first line of evidence deals with patterns of correlation among freshwater survival-rate indices of different stocks and among their marine survival-rate indices. If one of these life stages was mostly responsible for the regional covariation in SR indices, then we would expect consistent, strong, positive covariation among stocks in their survival-rate indices of that life stage. This analysis was restricted to the Bristol Bay region because it is the only region with smolt data for more than one stock. Here, correlations among the four indices of freshwater productivity were inconsistent, with an average correlation of 0.08 (Table 2A). In comparison, the average of the 28 correlations among Bristol Bay *marine* indices, lined up by ocean-entry year (OEY), was 0.35 (Table 2B). Twenty-four of these 28 correlations were positive (signs test, $P < 0.01$), with five being significant ($P < 0.05$). Furthermore, the average of the 12 correlations among marine indices of smolts that share both a common brood year and OEY (i.e., among age-1 smolts and among age-2 smolts) was 0.43. For comparisons between age-1 and age-2 marine indices, the average correlation by OEY was 0.28 (15 of 16 correlations positive; signs test, $P < 0.01$), while in contrast, the average correlation for these indices aligned by brood year (where these smolts enter the ocean in different years) was only –0.04 (7 of 16 correlations positive). Thus, the stronger pattern of covariation observed among the marine survival-rate indices than among the freshwater indices combined with the larger correlations when marine indices shared a common ocean-entry year suggest that the early marine life stage may be largely responsible for the covariation observed among the SR indices of Bristol Bay stocks.

The second line of evidence concerning sources of covariation in SR indices compared correlations between the survival indices of each life stage and a given stock's SR index. If the correlation between one life-stage's survival index and the stock's SR index is high, then it is more likely that covariation among SR indices would originate during that life stage. Unfortunately, a clear picture does not emerge for Bristol Bay stocks. The correlation between the Kvichak marine survival-rate index and its SR index was larger than the correlation between its freshwater and SR indices (Table 3). However, for the Ugashik and Wood stocks, both the marine and freshwater indices had similar correlations with the SR index, while for Egegik, the freshwater index was more strongly correlated with the SR index than was the marine index (Table 3). Thus, there was no consistent result that either the freshwater or marine life stage was the dominant source of variability for Bristol Bay stocks; therefore, this second line of evidence sheds little light on the cause of the covariation among overall SR indices of this region.

Table 3. Correlations between the freshwater and marine survival-rate indices of a given stock and the SR index of that stock. Note that where applicable, marine indices were calculated using both age-1 and age-2 smolts of the same brood year.

Stock	Years of data	Correlation between the SR index and: freshwater index	Correlation between the SR index and: marine index
Egegik	12	0.56	0.07
Kvichak	21	0.34	0.74
Ugashik	9	0.64	0.56
Wood	16	0.70	0.56
Skeena	33	0.47	0.64
Chilko	40	0.40	0.86

The third line of evidence examined correlations between a stock's freshwater (or marine) index and the region's aggregated SR index (calculated excluding that stock). If either life stage was the dominant source of the covariation, then we would expect a high correlation between the survival-rate index of that life stage and the aggregated SR index and a poor correlation for the other life stage. Once again, however, a clear picture does not emerge for Bristol Bay stocks. For example, the marine index of the Kvichak stock was more highly correlated with the aggregated Bristol Bay SR index ($r = 0.54$, $P = 0.01$) than was the freshwater index ($r = 0.11$), and notably, the Kvichak SR index was strongly correlated with the aggregated Bristol Bay SR index ($r = 0.69$, $P < 0.001$, Table 4). In contrast, for the Wood stock, which also had a strong correlation between its SR index and the aggregated Bristol Bay SR index ($r = 0.82$, $P < 0.001$), the freshwater index was slightly more strongly correlated with the aggregated SR index ($r = 0.50$, $P = 0.05$) than was the marine index ($r = 0.42$, Table 4). Across all four Bristol Bay stocks, the average correlations between the freshwater and marine indices and the aggregated SR indices were 0.24 and 0.51, respectively. Thus, this line of evidence suggests that the covariation among SR indices of Bristol Bay stocks stems from a combination of variation in survival rates in both the freshwater and, to a greater extent, marine life stages.

We did an analysis similar to the second and third lines of evidence for the Fraser River system, but only the Chilko stock had smolt data. The marine survival-rate index for the Chilko stock was more highly correlated with the SR index of this stock ($r = 0.86$) than was the freshwater index ($r = 0.40$), indicating that the marine life stage accounted for a

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Table 4. Correlations among the freshwater, marine, and spawner-to-recruit (SR) indices of survival rate of a given Bristol Bay stock and the aggregated SR index computed for all other Bristol Bay stocks.

		Correlation between aggregated SR index of stocks of the Bristol Bay region and		
Stock	Years of data	freshwater index	marine index	SR index of the stock
Egegik	12	0.10	0.64*	0.16
Kvichak	21	0.11	0.54*	0.69*
Ugashik	9	0.23	0.40	0.45
Wood	16	0.50*	0.42	0.82*

Note: * denotes correlations that are significant ($P < 0.05$).

greater proportion of the variability in overall survival rate (Table 3). Furthermore, the correlation between Chilko SR index and the aggregated SR index for Fraser River stocks (computed without the Chilko stock) was 0.32 ($P = 0.04$). The correlation between the aggregated Fraser SR index and Chilko freshwater index was –0.24, while the correlation with the Chilko marine index was 0.48 ($P = 0.002$). Thus, the relatively strong correlation between the aggregated Fraser SR index and our only measure of marine survival rate for a Fraser sockeye stock suggests that the little covariation that does exist among the Fraser stocks may occur during the early marine life stage, where smolts of different stocks share a common environment. These results for the Chilko stock were virtually the same when the aggregated Fraser SR index was recalculated using only the other 7 most abundant stocks described above.

These analyses for assessing the relative importance of the freshwater and marine life stages as sources of covariation must be interpreted cautiously. In the case of Bristol Bay stocks, it is not clear whether the lack of consistency among correlations between each stock's freshwater and marine survival-rate indices and its SR index (Table 3) or the region's aggregated SR index (Table 4) is due to real heterogeneity among stocks or to the relatively short smolt data series and the consequent wide sampling distribution for correlations. Moreover, there was limited power to detect a consistent pattern of positive correlations among the freshwater indices of Bristol Bay stocks, for which only 6 correlations could be calculated (Table 2A), in comparison to marine indices, where there were 28 correlations (Table 2B). In the case of Fraser River stocks, our inferences are particularly cautious given that smolt data, albeit a lengthy time series, were only available for the Chilko stock.

Another reason for cautious interpretation is that regional covariation among marine survival rates may be due in part to freshwater conditions. Variation in smolt body size has been shown to be an important determinant of marine survival rate (e.g., Koenings et al. 1993). Smolt body size is influenced by freshwater lake conditions that affect growth such as water temperature, prey supply, and juvenile abundance (Hume et al. 1996). Although our marine survival-rate indices accounted for changes in smolt abundance, which likely removed much of the stock-specific variation in marine survival associated with density-dependent effects on freshwater growth, it is possible that other regional-scale environmental processes, such as those noted above that could be common to nearby lakes, may have affected smolt body size and resulted in some of the covariation observed among marine survival rates.

Nevertheless, it appears that the observed covariation in overall (SR) survival-rate indices among sockeye salmon stocks of Bristol Bay is due to a combination of variation in both freshwater and, in particular, early marine survival rates, whereas the limited data on Fraser River stocks suggests that marine survival rates are most important. However, no single life stage dominates in driving that covariation for all stocks. To put these results into a broader context, note that the existing literature on Pacific salmon recognizes that both freshwater and marine life stages give rise to important sources of interannual variability in survival rate from eggs to recruits (Bradford 1995). For sockeye salmon, Bradford (1995) found that freshwater (egg-to-smolt) and marine (smolt-to-recruit) lifestages account for 43% and 57% of the variance over time in $\log_e$(recruits per spawner), respectively. Using our survival-rate indices, which corrected for possible density-dependent interactions (unlike those of Bradford), we found that for the six stocks with smolt data (Table 3), the average correlation between the freshwater survival-rate index and the SR index was 0.53, while the average correlation between the marine and SR indices was 0.62. Our results thus corroborate and extend Bradford's findings; freshwater and marine sources of variability are each important in our stocks. Furthermore, much of the variability in the survival-rate index from the spawner-to-recruit stage in our sockeye salmon stocks occurs during periods of their life history that are (*i*) unique (rather than common) to stocks of a given region and (*ii*) unique to individual stocks within a region, especially for Fraser stocks where correlations among SR indices were weak.

"Decadal-scale" patterns

Environmentally driven processes can influence survival rates at various time scales, including rapid between-year changes, those that occur slowly over a long period, and changes at intermediate time scales such as those commonly referred to as "decadal-scale" changes (Ware 1995). An example of the latter is a "regime shift" (Isaacs 1976), where some variable such as abundance or survival rate changes rapidly to a new level, which is maintained for a decade or two. Recent literature contains considerable discussion about a "regime shift" in climatic conditions and related physical and biological variables that occurred in the North Pacific in the mid-1970s (e.g., Venrick et al. 1987; Graham 1994), as well as its possible link to increased salmon productivity (e.g., Beamish 1993; Hare and Francis 1995; Adkison et al. 1996; Beamish et al. 1997; Mantua et al. 1997). These researchers reached varying conclusions about which salmon stocks were affected by the climate shift and by how much.

Unlike most of those studies, which mainly used data on catch or total abundance of recruits as indices of productivity (the exception was Adkison et al. 1996), our indices of survival rate allowed us to compare how various Alaska and B.C. sockeye stocks responded to the mid-1970s climatic shift without the potential confounding caused by changes in

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spawner abundance, which can affect catch and total recruitment even in the absence of a change in recruits per spawner. Figure 2 shows aggregated SR indices for Bristol Bay and Fraser River stocks (i.e., brood-year averages of each stock-specific SR index standardized to have unit variance), along with the standardized SR indices of the Cook, Copper, Nass, and Skeena stocks. For each SR index, we used intervention (step) analysis (Noakes 1986; Hare and Francis 1995) — a method that accounts for residual autocorrelation when testing hypothesized changes in mean levels of a time series — to determine whether long-term changes in the SR index occurred concurrently with the observed shift in climatic variables. Selecting time periods of brood years for these comparisons was based on physical and biological information. It has been clearly documented that a major shift towards high sea-level pressures and associated conditions in the central North Pacific Ocean began in the winter of 1946–1947 and persisted until the winter of 1976–1977, at which time a period of opposite conditions followed until at least the late 1980s (Trenberth and Hurrell 1995; Hare and Francis 1995; Mantua et al. 1997). Smolts that entered the ocean in the spring of 1976 (i.e., age-1 smolts of brood year 1974 and age-2 smolts of brood year 1973) would have experienced during their first year at sea the altered marine conditions that started in the winter of 1976–1977. Therefore, we initially tested for changes in mean productivity beginning with the 1973 brood year for all Alaska stocks and the Nass stock, which can have large numbers of age-2 smolts, and beginning with the 1974 brood year for Fraser River stocks and the Skeena stock, which have predominantly age-1 smolts. For most survival-rate time series that we examined, little autocorrelation was present and thus the appropriate intervention model was equivalent to a simple two-sample *t*-test. In all other cases, in particular for several Bristol Bay SR indices, the best intervention model was based on an AR(1) model.

The aggregated SR index for Bristol Bay stocks (Fig. 2A) shows a distinct shift from generally low productivity (unusually low numbers of recruits produced per spawner after correcting for density dependence) in brood years 1956 to 1972 to much higher average productivity from brood years 1973 through 1991 ($P < 0.001$). This pattern of increased productivity was a common feature of each of the nine Bristol Bay SR indices (Fig. 3), seven of which showed significant ($P < 0.05$) increases in SR residuals in the post-1972 period, indicating that similar mechanisms were involved in each case. In terms of the Ricker model, these shifts in residuals correspond to increases in the modal recruitment per spawner (R/S), for any specified spawner abundance, ranging from 48% (Naknek) to 214% (Ugashik), with an average increase across the nine Bristol Bay stocks of 109%. Qualitatively similar results were found for intervention models where the hypothesized shift in productivity first began in either the 1972 or 1974 brood year.

The SR indices for the Cook, Copper, Nass, and Skeena stocks also showed increases in the recent period, but to varying degrees (Figs. 2B–2E). It is particularly difficult to assess the possible influence of the climate shift of the mid-1970s on the Cook and Nass stocks given the limited number of data points before then. For the Cook, Copper, and Nass stocks, productivity increased in the post-1972 period, although these changes were not significant. There was a significant increase ($P = 0.002$) in the SR residuals of the Skeena stock beginning with brood year 1974 (Fig. 2E), representing an 87% increase in modal R/S; however, this may be largely due to increases in freshwater productivity through enhancement by spawning channels that were completed in 1971 (McDonald and Hume 1984). Indeed, intervention analysis of the freshwater survival-rate index (brood years 1959–1992) of the Skeena stock showed a large increase in the post-1973 period ($P < 0.01$), while the marine survival-rate index had only a slight increase ($P = 0.46$).

In contrast with these other stocks, particularly the Bristol Bay stocks, the SR indices of Fraser River stocks do *not* show a consistent pattern of improved productivity beginning in the mid-1970s. In fact, for the aggregated Fraser SR index, there was a slight, but non-significant, decrease ($P = 0.13$) beginning in brood year 1974 (Fig. 2F). Moreover, the 16 Fraser stocks exhibit a wide range of patterns in SR residuals (Fig. 4), with only three of the stock-specific interventions being significant ($P < 0.05$), all of which represented decreases in productivity (Early Stuart, Nadina, and Pitt). In addition, there was an increase in the marine survival-rate index of the Chilko stock (brood years 1949–1988) in the post-1973 period, although not significant ($P = 0.23$).

As noted by Beamish et al. (1997), there is evidence of a sharp decline in productivity for many Fraser River sockeye stocks beginning with the 1990 brood year (Figs. 2F and 4), which they speculate may be associated with another change in climatic conditions (Trenberth and Hurrell 1995; Mantua et al. 1997). However, note that the non-Fraser B.C. stocks and the Alaskan stocks do not show similar declines (Figs. 2 and 3). Nevertheless, to determine the influence of the 1990–1992 brood years on our results for Fraser SR indices, we repeated the intervention analyses excluding those years. In general, mean levels of productivity associated with the post-1973 period increased slightly when the last 3 years were omitted, but only the Birkenhead stock showed a significant increase at $P < 0.05$. These latter intervention models implied changes in modal R/S ranging from –45% for Pitt (i.e., a decrease in productivity in the post-1973 period) to +49% for Birkenhead, with an average across all 16 Fraser stocks of –6%, or just +11% for the eight most abundant Fraser stocks noted previously. In all cases, similar results were obtained for intervention models where the hypothesized shift in productivity first began in the 1975 brood year instead of 1974.

We conducted a final set of intervention analyses for Bristol Bay and Fraser River stocks to determine if the way that we calculated our indices of survival rate may have masked some evidence of increased productivity. Specifically, if lengthy periods of increased productivity (recruits per spawner at a given spawner abundance) coincide with increases in spawner abundances in the stock-recruit data set, then a Ricker model fit to the entire data set will likely be biased too flat (Walters 1990). This could alter the pattern of residuals estimated from the regression by, for example, attributing high survival rates at large spawner abundances to an apparent lack of density dependence, rather than to favorable environmental conditions. Thus, to compare our previous approach with this one, we fit the Ricker model for each

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Fig. 2. Time series of aggregated spawner-to-recruit (SR) indices for Bristol Bay stocks (A) and for Fraser River stocks (F), and standardized SR indices for the Cook (B), Copper (C), Nass (D), and Skeena stocks (E). Interventions (horizontal lines) and corresponding *P*-values are shown for tests of hypothesized shifts in mean levels of each survival-rate index beginning with the 1973 brood year (Bristol Bay, Cook, Copper, and Nass) or 1974 brood year (Skeena and Fraser River). SR indices are residuals from the best-fit Ricker models. See text for details.

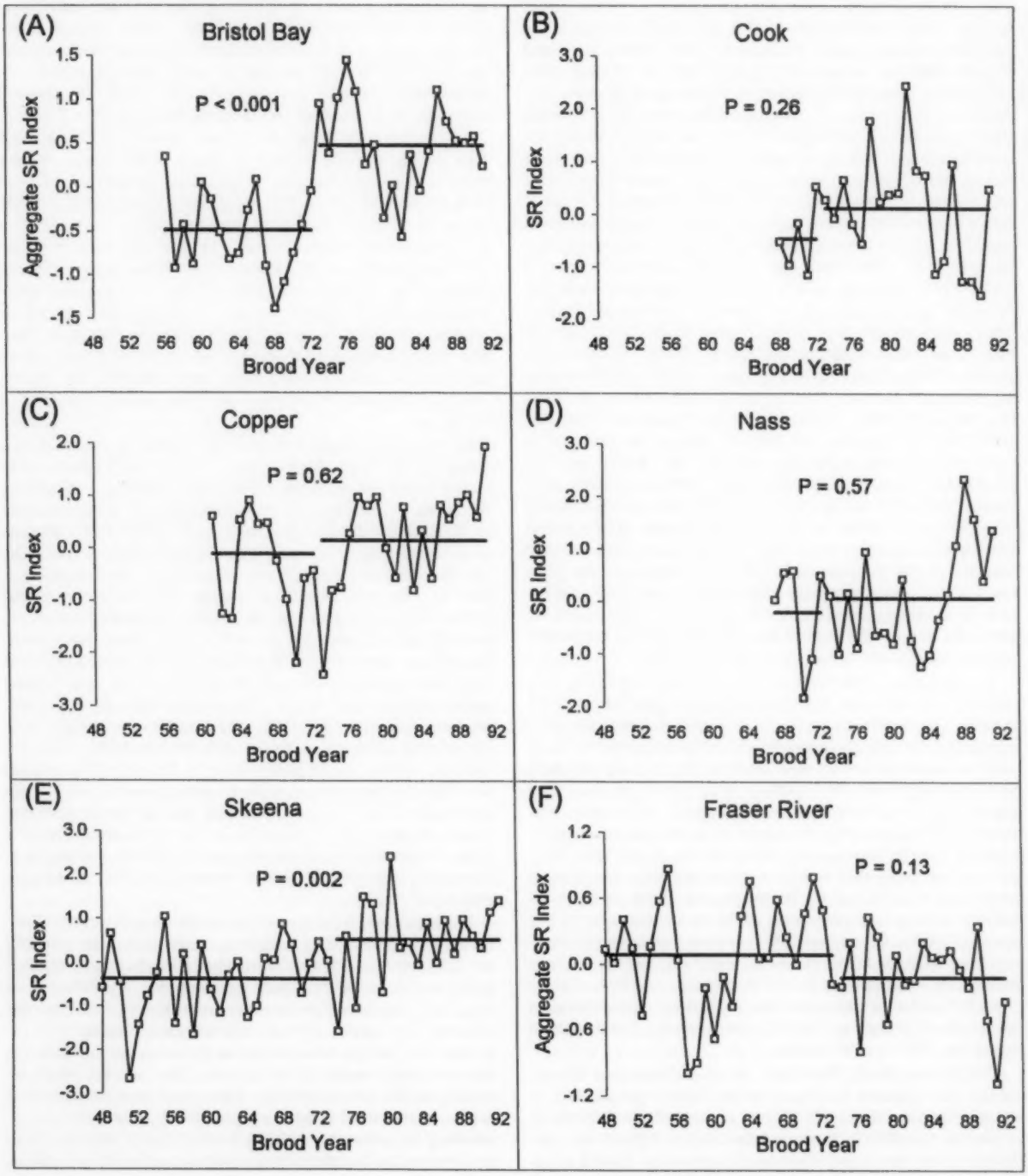

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Fig. 3. Time series of standardized spawner-to-recruit (SR) indices for the nine Bristol Bay stocks. Interventions (horizontal lines) and corresponding *P*-values are shown for tests of hypothesized shifts in mean levels of each survival-rate index beginning with the 1973 brood year. See text for details.

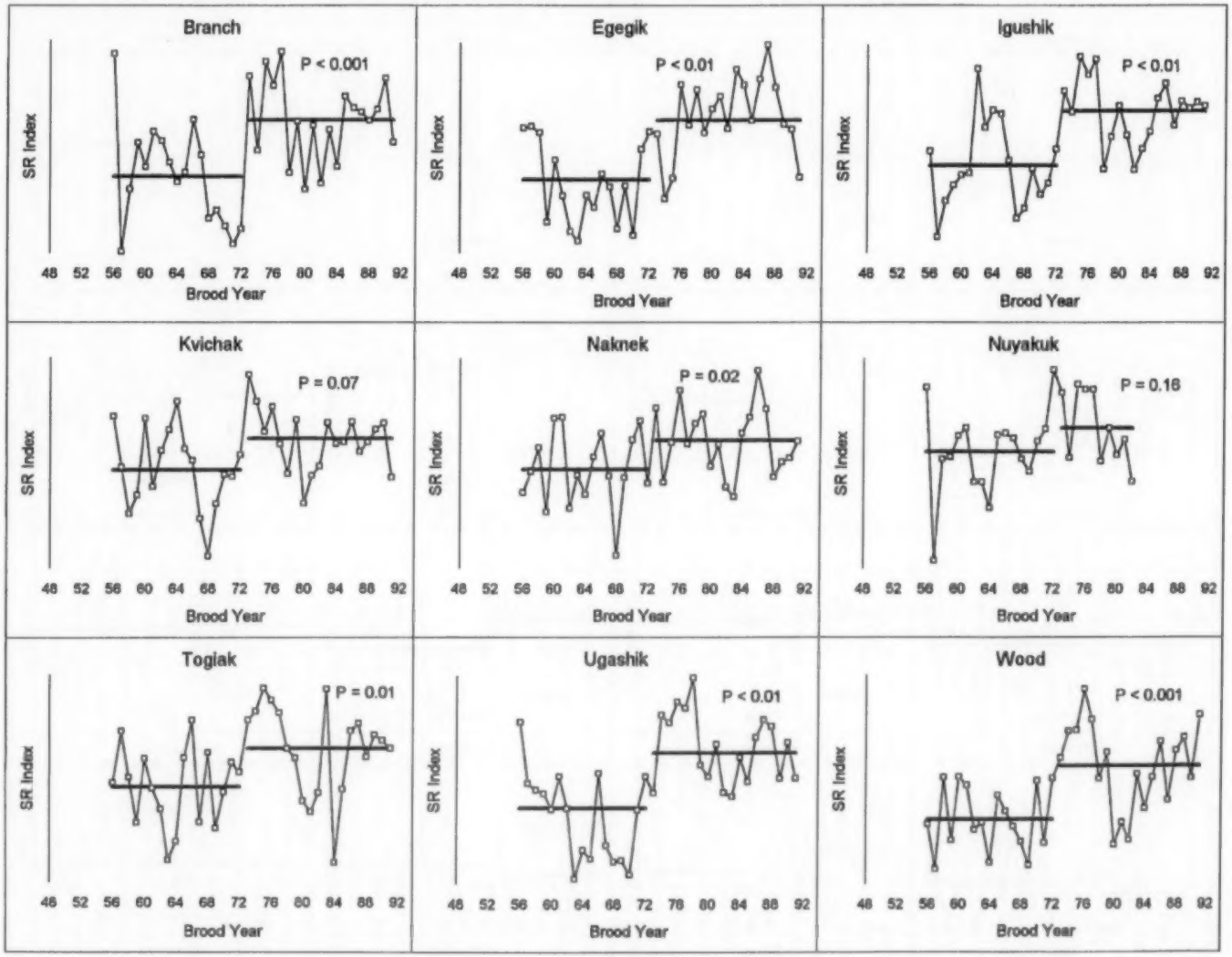

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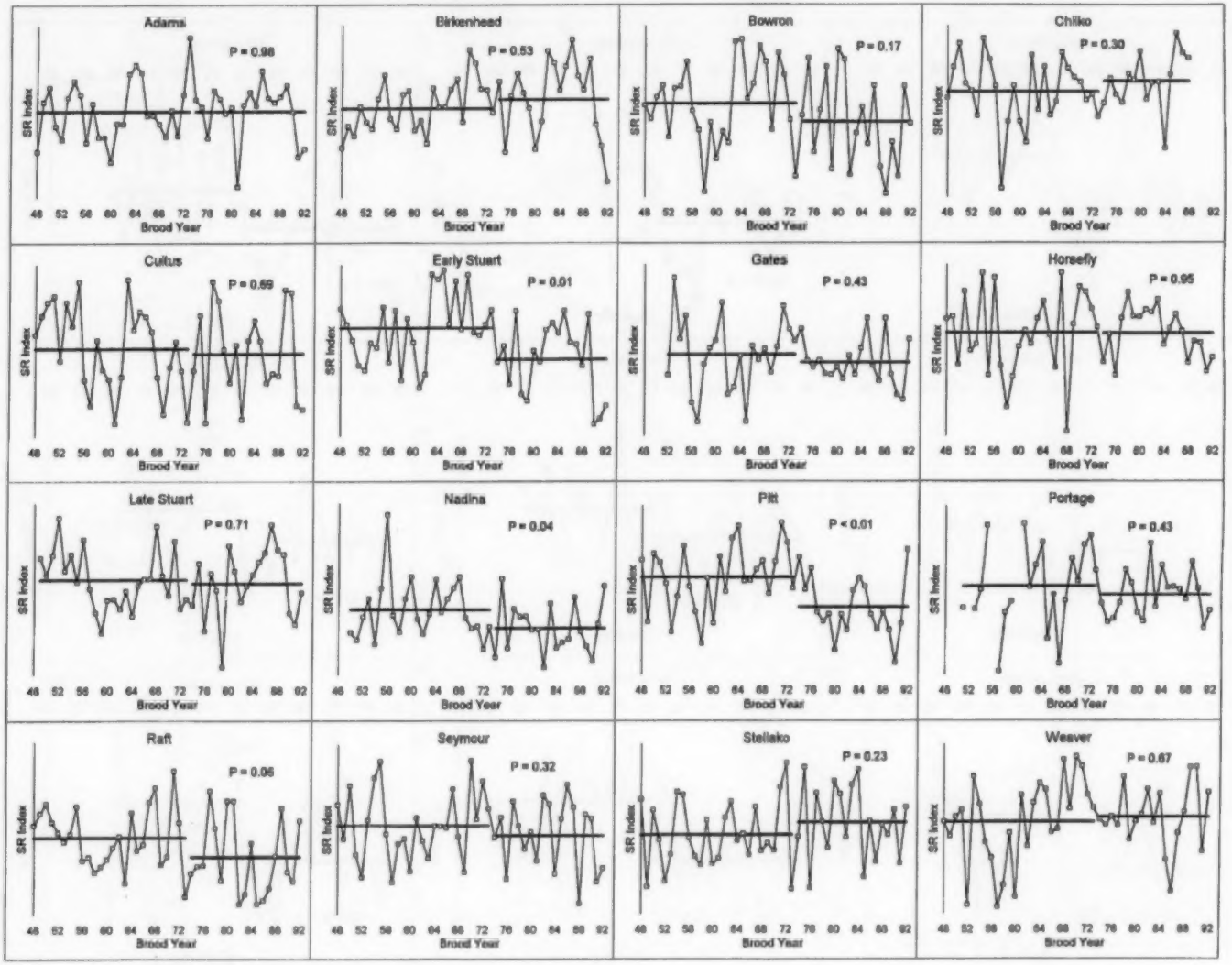
Fig. 4. Time series of standardized spawner-to-recruit (SR) indices for the 16 Fraser stocks. Interventions (horizontal lines) and corresponding *P*-values are shown for tests of hypothesized shifts in mean levels of each survival-rate index beginning with the 1974 brood year. See text for details.



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stock to *only* those brood years before the hypothesized shift in productivity and then estimated the residuals for *all* brood years from this fit.

For all Bristol Bay stocks and most Fraser River stocks, these new patterns of residuals and results of intervention analyses were very similar to those reported above. There were notable differences for the new residuals of the Weaver and Horsefly stocks, which showed much greater changes in the post-1973 period (excluding brood years 1990–1992), representing increases in modal *R/S* of 140% ($P = 0.04$) and 40% ($P = 0.26$), respectively (versus 8% and 10% estimated for the original SR indices). Overall, however, only 9 of the 16 Fraser stocks showed increases in productivity in the post-1973 period, and there was again little evidence of a consistent pattern of response across Fraser stocks as would be expected if a similar environmental mechanism(s) associated with the climatic shift of the mid-1970s was an important determinant of survival rates of each of these stocks.

In addition, after the potential effects of a regime shift in productivity were removed from each SR index, we found that patterns of covariation among Alaskan and B.C. stocks were very similar to those reported above but weaker for comparisons among the nine Bristol Bay stocks. Specifically, we computed correlations among the residuals of the best-fit interventions for each stock's SR index (Figs. 2–4). These correlations were similar in magnitude and sign to those for the original SR indices (Table 1) for all comparisons involving the Cook, Copper, Nass, Skeena, and Fraser River stocks. However, among the nine Bristol Bay stocks, the average correlation was reduced from 0.44 for the original SR indices to 0.26 for the regime-shift residuals, and the number of significant positive correlations was reduced from 21 to 9. Thus, it is clear that the decadal-scale changes in mean productivity shared by Bristol Bay SR indices were an important source of covariation among them. In contrast, there was little evidence that coincident shifts in productivity were important sources of covariation between Bristol Bay SR indices and those of the other Alaskan or B.C. stocks or that these shifts masked patterns of interannual covariation between them.

The intervention results suggest that the decadal-scale environmental changes that occurred in the mid-1970s mainly improved productivity for sockeye stocks that entered the ocean in northern areas, particularly Bristol Bay stocks, while for those that entered further south, such as Fraser River stocks, the effect was on average much smaller and more variable among stocks. These findings are consistent with those from other research that found dramatic and persistent increases in productivity of Bristol Bay sockeye salmon (Adkison et al. 1996; Hare 1996) but not for Fraser River stocks (Adkison et al. 1996). These results are also consistent with the hypothesis that there were differences from north to south in oceanographic conditions that could affect survival of salmon stocks (Cheiton 1984; Mantua et al. 1997; Schwing et al. 1997). In short, our results on patterns of covariation, combined with the regime shift analysis, suggest that survival rates of Bristol Bay and Fraser River stocks are influenced by processes that operate not only at different spatial scales, but also at different time scales. Survival rates of Fraser River stocks appear to be driven primarily by large, stock-specific interannual variability as well as some common variability among stocks, while Bristol Bay stocks are influenced by stronger regional-scale processes acting at both interannual and decadal time scales.

In contrast, Beamish and Bouillon (1993) and Beamish et al. (1997) reached a different conclusion regarding spatial and temporal scales of important environmental processes. Specifically, they concluded that there was a clear synchronous trend towards increased productivity of both Fraser River and Bristol Bay sockeye salmon, which they attributed to the common effect of ocean-basin, decadal-scale changes in environmental conditions linked to the climatic shift of the mid-1970s. This difference between our findings may be explained by the type of data used. First, we focused on stock-specific indices of survival rate, while their conclusions on this specific topic relied largely on catch and total recruitment data pooled across stocks. As we have emphasized, our SR indices of survival rate avoid the potential confounding of changes in spawner abundance and should therefore be a better measure of changes in productivity caused by environmental processes. Indeed, the average stock-specific correlation between annual abundances of recruits and the SR index used here was only 0.45 for Fraser River stocks and between 0.49 and 0.66 for non-Fraser stocks (nearly identical correlations were found using annual catches). Thus, recruitment or catch data reflect only 20–44% of the variance in productivity of these stocks as we have measured it (i.e., residuals in $\log_e$(recruits/spawner) from the best-fit stock-recruitment relationship). Second, Beamish et al. (1997) used as part of their evidence a single, Fraser River system-wide stock-recruitment relationship, which may not be representative of many of these stocks, whereas we base our conclusions solely on a comparison of survival-rate indices estimated from numerous stock-specific stock-recruitment relationships (e.g., Fig. 4).

Conclusions

Our results suggest that the shared environmental causes of variation in survival rates of sockeye salmon operate mainly on regional spatial scales (i.e., within Bristol Bay stocks and within Fraser River stocks). This is true for both relatively rapidly changing sources of variation on the interannual scale and those on the decadal scale. The limited evidence available suggests that these sources of environmental variation arise during early marine life (and to some extent in fresh water in the Bristol Bay stocks). Tests of specific environmental mechanisms affecting survival rates of sockeye salmon will be the subject of another paper.

Our results also support previous findings that there was a major increase in productivity of Bristol Bay sockeye salmon stocks beginning in the 1970s. This increased productivity may or may not persist. Therefore, fishery management strategies, as well as economic investment plans by industry, should recognize the unusual nature of the last two decades for these stocks and should take appropriate precautionary actions. Indeed, to the extent that regional covariation among survival rates of Pacific salmon is driven by persistent changes in the environment, independently of management actions such as enhancement and harvesting, then future changes in productivity may be common to many stocks within a region. Thus, fishing opportunities within a

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region may tend to increase or decrease across many stocks together, producing a region-wide "boom," as was seen in the 1980s in Bristol Bay, Alaska, or a "bust," as in Oregon and Washington (although the latter was confounded by harvesting and changes in habitat).

Finally, we plea for collection of more extensive data on abundance of early life stages of Pacific salmon. One major reason why it is so difficult to understand the causes of spatial and temporal trends in survival rates, and to deal effectively with their management implications, is the lack of long-term data across numerous stocks on survival rates in different life stages. Such data (derived from estimates of fry and smolt abundances) are seldom collected, and when they are, they are costly enough to be particularly vulnerable to cuts during budget restraints. We strongly recommend that despite budget cuts, management agencies continue to estimate abundance of fry or smolts annually. This will continue to build longer data series, permit more effective tests of hypotheses, and avoid creating inconclusive data sets that contain many years with missing data.

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References

Adkison, M.D., Peterman, R.M., Lapointe, M.F., Gillis, D.M., and Korman, J. 1996. Alternative models of climatic effects on sockeye salmon, *Oncorhynchus nerka*, productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. Fish. Oceanogr. **5**: 137–152.

Beamish, R.J. 1993. Climate and exceptional fish production off the west coast of North America. Can. J. Fish. Aquat. Sci. **50**: 2270–2291.

Beamish, R.J. (*Editor*). 1995. Climatic change and northern fish populations. Can. Spec. Publ. Fish. Aquat. Sci. No. 121.

Beamish, R.J., and Bouillon, D.R. 1993. Pacific salmon production trends in relation to climate. Can. J. Fish. Aquat. Sci. **50**: 1002–1016.

Beamish, R.J., Neville, C.M., and Cass, A.J. 1997. Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. Can. J. Fish. Aquat. Sci. **54**: 543–554.

Bocking, R.C., and Peterman, R.M. 1988. Preseason forecasts of sockeye salmon (*Oncorhynchus nerka*): comparison of methods and economic considerations. Can. J. Fish. Aquat. Sci. **45**: 1346–1354.

Bradford, M.J. 1995. Comparative review of Pacific salmon survival rates. Can. J. Fish. Aquat. Sci. **52**: 1327–1338.

Burgner, R.L. 1991. Life history of sockeye salmon. *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 1–117.

Cass, A.J., and Wood, C.C. 1994. Evaluation of the depensatory fishing hypothesis as an explanation for population cycles in Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **51**: 1839–1854.

Chelton, D.B. 1984. Commentary: short-term climatic variability in the Northeast Pacific Ocean. *In* The influence of ocean conditions on the production of salmonids in the North Pacific. *Edited by* W. Pearcy. Oregon State University Press, Corvallis, Oreg. pp. 87–99.

Collie, J.S., Peterman, R.M., and Walters, C.J. 1990. Experimental harvest policies for a mixed-stock fishery: Fraser River sockeye salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. **47**: 145–155.

Emmett R., and Schiewe, M.H. (*Editors*). 1997. Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. U.S. Dept. of Commerce, NOAA Tech. Memo. NMFS-NWFSC-29.

French, R., Bilton, H., Osaka, M., and Hartt, A. 1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 34.

Graham, N.E. 1994. Decadal-scale climate variability in the tropical and North Pacific during the 1970s and 1980s: observations and model results. Clim. Dynam. **10**: 135–162.

Groot, C., and Cooke, K. 1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 53–60.

Hare, S.R. 1996. Low frequency climate variability and salmon production. Ph.d. Dissertation. University of Washington, Seattle, Wash.

Hare, S.R., and Francis, R.C. 1995. Climate change and salmon production in the Northeast Pacific Ocean. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121. pp. 357–372.

Hume, J.M.B., Shortreed, K.S., and Morton, K.F. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. Can. J. Fish. Aquat. Sci. **53**: 719–733.

Isaacs, J.D. 1976. Some ideas and frustrations about fishery science. Calif. Coop. Oceanic Fish. Invest. Rep. **18**: 34–43.

Jenkins, G.M., and Watts, D.G. 1968. Spectral analysis and its applications. Holden-Day, San Francisco, CA.

Koslow, J.A., Thompson, K.R., and Silvert, W. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and environment. Can. J. Fish. Aquat. Sci. **44**: 26–39.

Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteor. Soc. **78**: 1069–1079.

Minard, R.E., and Meacham, C.P. 1987. Sockeye salmon (*Oncorhynchus nerka*) management in Bristol Bay, Alaska. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 336–342.

Myers R.A., Mertz, G., and Bridson, J. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Can. J. Fish. Aquat. Sci. **54**: 1400–1407.

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Noakes, D.L. 1986. Quantifying changes in British Columbia Dungeness crab (*Cancer magister*) landings using intervention analysis. Can. J. Fish. Aquat. Sci. **43**: 634–639.

Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle, Wash.

Peterman, R.M. 1982. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Can. J. Fish. Aquat. Sci. **39**: 904–913.

Peterman, R.M. 1987. Review of the components of recruitment of Pacific salmon. *In* Common strategies of anadromous and catadromous fishes. *Edited by* M. Dadswell, R. Klauda, C. Moffitt, R. Saunders, R. Rulifson, and J.E. Cooper. Am. Fish. Soc. Symp. No. 1. pp. 417–429.

Pyper, B.J., and Peterman, R.M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. Can. J. Fish. Aquat. Sci. **55**: 2127–2140.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191. pp. 1–382.

Ricker, W.E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Board Can. **33**: 1483–1524.

Schwing, F.B., Parrish, R., and Mendelssohn, R. 1997. Decadal-scale environmental variability in the coastal Northeastern Pacific. *In* Estuarine and ocean survival of Northeastern Pacific salmon: Proceedings of the workshop. *Edited by* R. Emmett and M.H. Schiewe. U.S. Dept. of Commerce, NOAA Tech. Memo. NMFS-NWFSC-29. pp. 105–111.

Straty, R.R. 1974. Ecology and behaviour of juvenile sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay and the eastern Bering Sea. *In* Oceanagraphy of the Bering Sea with emphasis on renewable resources. *Edited by* D.W. Hood and E.J. Kelley. Univ. Alaska Inst. Mar. Sci. Occ. Publ. 2.

Thompson, K.R., and Page, F.H. 1989. Detecting synchrony of recruitment using short, autocorrelated time series. Can. J. Fish. Aquat. Sci. **46**: 1831–1838.

Trenberth, K.E., and Hurrell, J.W. 1995. Decadal coupled atmosphere–ocean variations in the North Pacific Ocean. *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. 121. pp. 15–24.

Venrick, E.L., McGowan, J.A., Cayan, D.A., and Hayward, T.L. 1987. Climate and chlorophyll *a*: long-term trends in the central North Pacific Ocean. Science (Washington, D.C.), **238**: 70–72.

Walters, C.J. 1990. A partial bias correction factor for stock-recruitment parameters in the presence of autocorrelated environmental effects. Can. J. Fish. Aquat. Sci. **47**: 516–519.

Walters, C.J., and Collie, J.C. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. **45**: 1848–1854.

Walters, C.J., and Staley, M.J. 1987. Evidence against the existance of cyclic dominance in Fraser River sockeye salmon (*Oncorhynchus nerka*). *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. 96. pp. 375–384.

Ware, D.M. 1995. A century and a half of change in the climate of the NE Pacific. Fish. Oceanogr. **4**: 267–277.

Ware, D.M., and MacFarlane, G.A. 1989. Fisheries production domains in the Northeast Pacific Ocean. *In* Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. *Edited by* R.J. Beamish and G.A. MacFarlane. Can. Spec. Publ. Fish. Aquat. Sci. No. 108. pp. 359–379.

Zar, J.H. 1984. Biostatistical analyses. Prentice-Hall, Englewood Cliffs, N.J.

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PERSPECTIVE

Ontogeny of energetic relationships and potential effects of tissue turnover: a comparative modeling study on lake trout

Jixiang He and Donald J. Stewart

Abstract: Tissue turnover is endogenous energy flow and may play a regulatory role in the metabolic system of an organism. We developed a general growth model addressing potential effect of tissue turnover on energy acquisition and partitioning. We applied the model to estimate energy assimilation of lake trout (*Salvelinus namaycush*) in Lake Michigan and compared the model with a commonly used complex model. Both models are expansions of the Pütter – von Bertalanffy growth model. The new model suggested a consistent decreasing trend in energy net conversion efficiency (NCE) for somatic growth versus body energy. The complex model suggested that NCE is relatively stable in early ages and decreases slowly in comparison with the pattern suggested by the new model. The new model estimated higher specific assimilation rate and NCE for gonadal growth than for somatic growth of mature fish. The complex model did not distinguish gonadal growth from somatic growth. For a lake trout growing from the start of age-1 to the end of age-10, our new model suggested a total energy assimilation 25% higher than the complex model. The above comparisons support the inference that tissue turnover is an important bioenergetic component. Inclusion of tissue turnover in bioenergetic modeling analyses may be critical for studying the linkages among individual growth, reproduction, and population dynamics.

Résumé : Le renouvellement tissulaire constitue un flux d'énergie endogène et peut jouer un rôle régulateur dans le métabolisme d'un organisme. Nous avons élaboré un modèle général de croissance traitant de l'effet potentiel du renouvellement tissulaire sur l'acquisition et la répartition de l'énergie. Nous avons appliqué le modèle au calcul de l'assimilation de l'énergie chez le touladi (*Salvelinus namaycush*) du lac Michigan, et nous l'avons comparé à un modèle complexe couramment employé. Ces deux modèles sont des adaptations du modèle de croissance de Pütter – von Bertalanffy. Le nouveau modèle met en évidence une tendance constante à la baisse du rendement net de conversion de l'énergie (RNC) quand on considère la croissance somatique par rapport à l'énergie corporelle. Le modèle complexe fait ressortir le fait que le RNC est relativement stable dans les premières phases puis baisse lentement si on le compare au régime indiqué par le nouveau modèle. Ce dernier donne une estimation plus élevée du taux d'assimilation spécifique et du RNC pour la croissance gonadique que pour la croissance somatique des poissons à maturité. Le modèle complexe ne faisait pas de différence entre la croissance gonadique et la croissance somatique. Pour un touladi dont on suit la croissance du début de l'âge-1 jusqu'à la fin de l'âge-10, notre nouveau modèle suggère que l'assimilation totale de l'énergie est de 25 % supérieure aux résultats du modèle complexe. Les comparaisons ci-dessus viennent confirmer que le renouvellement tissulaire est une composante bioénergétique importante. L'intégration du renouvellement tissulaire dans les analyses de modélisation pourrait jouer un rôle crucial dans l'étude des liens entre la croissance des individus, la reproduction et la dynamique des populations.

[Traduit par la Rédaction]

Introduction

There have been two types of models for studying the energetic basis of fish growth (Adams and Breck 1990; Ney 1990; Gerking 1994). One uses data on the daily cycle of food mass in fish stomachs and evacuation rates (Bajkov 1935; Eggers 1977; Elliott and Persson 1978). The other is based on fish energy balance (Clarke et al. 1946; Winberg 1956). The second approach includes a variety of energetic models, and the modelers attempt to study mechanisms that regulate organismal growth (Ivlev 1945; Paloheimo and Dickie 1965; Gerking 1994). The empirical basis for those models had been summarized by the end of the 1970s (Brett and Groves 1979), while a biological understanding still required more advanced studies (Ricker 1979).

One extreme of the second approach is to use simple growth models and explore their energetic implications (von Bertalanffy 1957; Pauly 1986), while another extreme is to

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model complex energetic components with as much detail as needed for a particular application (Kitchell et al. 1977; Stewart et al. 1983; From and Rasmussen 1984; Stewart and Binkowski 1986; Brandt et al. 1992). Between those extremes, there are many studies that either aggregate bioenergetic components (Mann 1965; Majkowski and Hearn 1984) or combine a simple growth model with radiotracer techniques (Forseth et al. 1992; Rowan and Rasmussen 1996). Comparing various energetic models can improve our understanding of organismal growth and food web dynamics (Boisclair and Leggett 1989). Since Ursin's (1979) work, however, few studies have attempted to bridge the two extremes and compare models by explicitly analyzing both model results and model structure.

Over the past 20 years, there have been advances in experimental studies about the relationships between protein turnover and energetics (Houlihan 1991; Hawkins 1991). The implications of those experimental studies have not been integrated into either simple or complex energetic models. Protein turnover is intracellular protein degradation to amino acids and protein renewal (Hawkins 1991). A related phenomena is seasonal dynamics of body energy density, which in turn, is a key component of reproduction processes and seasonal mortality patterns (Flath and Diana 1985; Diana and Salz 1990). In early life stages, protein turnover related to energetic constraints also influences fish mortality and recruitment processes (Blaxter and Hempel 1963; Miller et al. 1988). Although the exact linkage between protein turnover and energy turnover is not clear yet, we anticipate that total tissue turnover is a key component for extending commonly used energetic models (e.g., Kitchell et al. 1977; Stewart et al. 1983) to study fish life histories and population dynamics.

In this paper, our objective is to develop an energetics-based growth model that includes effects of tissue turnover on the specific rate of energy assimilation and energy net conversion efficiency (NCE). Such a development allows for addressing linkages and differences between somatic and gonadal growth. To maintain a focus on available empirical observations and address integrative feedback mechanisms, we develop our model by combining the simple models of Pütter – von Bertalanffy (Pütter 1920; von Bertalanffy 1957) and Pauly (1986) with a more general structure. To evaluate the advantages of addressing the potential effects of tissue turnover, we apply our model to lake trout (*Salvelinus namaycush*) in Lake Michigan and compare our model with a commonly used complex model (Stewart et al. 1983).

Complexity of fish energetics and the importance of tissue turnover

Complex fish energetic models are reinterpretations and expansions of the simple Pütter – von Bertalanffy model (Ursin 1979; From and Rasmussen 1984):

$$\text{Growth} = \text{assimilation} - \text{respiration}$$
$$= \text{consumption} - \text{egestion} - \text{excretion} - \text{respiration}$$

Those expansions assume that relationships among various energetic components are simply additive. When more and more details have been included, the additive expansions reveal their current limitations for expressing integrative regulatory mechanisms. Recent debates about model structure and applications have focused on submodels of respiration, including basal respiration, activity-related respiration, and specific dynamic action (SDA) (Boisclair and Leggett 1989). There are direct correlations among consumption, growth, and activity-related respiration (Kerr 1982, Boisclair 1992; Björnsson 1993; Madon and Culver 1993). Specific dynamic action is primarily related to growth, while processing food and eliminating excreta only account for a very small part of SDA (Ashworth 1969; Tandler and Beamish 1979; Jobling 1983; Brown and Cameron 1991*a*, 1991*b*). Statistically, SDA is also correlated with food intake (Beamish 1974), food composition (Beamish and Trippel 1990), body mass (Beamish and Trippel 1990), and even activity (Krohn et al. 1997).

The foregoing multiple correlations support an inference that total respiration is quantitatively not divisible (Jobling 1981, 1983). Experiments for estimating SDA used a condition in which activity-related respiration was a constant and would not be affected by feeding (Beamish 1974; Beamish and Trippel 1990). An estimated relation between activity-related respiration and consumption, however, had to assume that SDA was a constant proportion of consumption and was not related to feeding-induced activity (Kerr 1982). Experiments for estimating energetic costs of swimming excluded effects of both feeding-induced activities and SDA (Brett 1964; Rao 1968; Tytler 1969; Beamish 1970; Muir and Niimi 1972; Stewart et al. 1983); otherwise, the relationships of respiration to swimming speed would be different among periods of pre-feeding, feeding, and post-feeding (Durbin et al. 1981). Observations of the correlation between swimming and consumption did not consider the existence of SDA but had to use the results of the above-mentioned nonfeeding experiments to calculate swimming energetic costs (Boisclair 1992; Björnsson 1993). Even the concepts of maintenance respiration and the cost of growth have been often interpreted with ambiguities. Maintenance respiration was related to rebuilding of dead tissues or metabolic substance (Gerking 1962), and the cost of growth has been calculated as total respiration minus maintenance respiration. Recent studies indicated that the specific rate of tissue turnover increases with swimming activity and the specific rate of growth (Houlihan and Laurent 1987; Houlihan et al. 1988). Thus, if maintenance is an energetic component of a growth process, it must be larger than the basal respiration. Commonly used fish energetic models have adapted to our current incomplete understanding of the biological complexity. The estimation of activity-related respiration is independent of consumption, and the value of SDA is simply calculated as a proportion of absorbed exogenous energy (Kitchell et al. 1977; Stewart et al. 1983).

Tissue turnover is an important energetic component, but the above energy balance does not give it an explicit treatment. Von Bertalanffy (1957) explained growth as the difference between "building up" and "breaking down." His meaning was straightforward and did not explicitly address energy cost for building up and energy loss due to breaking down. The above reinterpretations and expansions of the Pütter – von Bertalanffy model actually followed Winberg's (1956) energy balance but apparently ignored details of tis-

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sue turnover that were covered by von Bertalanffy's (1957) original concept. In Gerking's (1962) study, when a bluegill sunfish (*Lepomis macrochirus*) grew from 17.5 g to 34.0 g, total protein synthesis was 7.87 g, protein turnover (replacement) was 5.06 g, and net protein growth was only 2.81 g. Based on small animal experiments, a recent general estimate is that 1 g of protein retention requires 2–4 g of protein synthesis (Waterlow 1995).

When food is sufficient and an organism is rapidly growing, endogenous excretion of nitrogen may be negligible (Hawkins 1985; Jayaram and Beamish 1992). If protein turnover is at least one to three times protein retention, breakdown materials must be recycled. Then, the net effect of tissue turnover is only an increase of respiration. Unfortunately, there have been no experiments that attempted to separate this increase from, or partition it into, SDA and activity-related respiration. There are seasonal dynamics of body energy density, and there is energy or protein loss due to reproduction. Thus, endogenous excretion is not negligible in natural conditions and materials from tissue turnover are not completely recycled, particularly for large-scale measurements such as yearly growth and energy assimilation. We cannot, however, add tissue turnover as a separate term into an energy balance unless future studies can explicitly quantify two components of the net effects of tissue turnover. One is material from tissue turnover that has not been recycled, and another is a part of respiration, which may or may not be covered by current formulations of SDA or activity-related respiration.

An alternative approach to address the above complexity is to properly aggregate detailed energetic components (Ney 1990). The basis for such an aggregation must be a reconsideration of energy or mass balance, because tissue turnover is endogenous and partially recycled flux inside the system boundary. Even when organisms increase their body mass with sufficient food, at least protein turnover is still occurring, and the specific rate of protein turnover is positively related to the specific rate of protein growth (Houlihan et al. 1988).

The positive relation between growth and tissue turnover indicates that endogenous energy flow may play a regulatory role as an organism adapts to an given environment or responds to environmental changes. In a given environmental setting, efficient organisms have a low ratio of protein turnover to protein synthesis and a high specific rate of growth (Hawkins et al. 1986; McCarthy et al. 1994). That is because of either relatively low basal metabolism or relatively slow increases in the specific rate of tissue turnover as specific growth rate increases. As body mass increases, the ratio of protein turnover to protein synthesis increases and the specific rate of growth decreases (Goldspink and Kelly 1984, Tables 1 and 2; Houlihan et al. 1986, Tables 2 and 3; Houlihan et al. 1988, Fig. 4). When body mass is close to its asymptotic value and the specific growth rate equals or is close to zero, tissue turnover will account for most of tissue synthesis.

Energetic basis of the simple model by Pütter – von Bertalanffy and Pauly

Before we address the above regulatory mechanism using an aggregated simple model, we need to provide further clarification of fundamental concepts. The basic equation of Pauly's (1986) model for estimating consumption is as follows:

$$\text{(1)} \qquad \text{GCE} = 1 - (W/W_a)^{\theta}$$

where GCE is gross conversion efficiency (growth/consumption), W is body mass, W_a is the asymptotic body mass, and θ is a nondimensional constant. When an increase in body mass (ΔW) has been measured, we may estimate consumption (g or J) in the growth period ($\Delta C/\Delta t$) using

$$\text{(2)} \qquad \Delta C/\Delta t = \Delta W/\text{GCE} = \Delta W/(1 - (W/W_a)^{\theta})$$

Here, we do not need to address the method for estimating θ value, because Pauly's model (eq. 1) is identical to the Pütter – von Bertalanffy model (Silvert and Pauly 1987):

$$\text{(3)} \qquad \Delta W/\Delta t = pW^M - qW^N$$

where pW^M refers to consumption rate ($\Delta C/\Delta t$), qW^N refers to the sum of nongrowth components in the consumption rate, p and M are regression parameters, $q = (p / W_a^{\theta})$, and $N = M + \theta$. In the following analysis, we use the specific rate of growth (dW/Wdt), so eq. 3 is rewritten as

$$\text{(4)} \qquad dW/Wdt = pW^m - qW^n$$

where $m = M - 1$ and $n = N - 1$. Based on eq. 4, Pauly's model (eq. 1) can be written in a more general form:

$$\text{(5)} \qquad \text{GCE} = 1 - xW^y$$

where $x = q/p$, and $y = (n - m)$. Usually, $n > m$ and $y > 0$, so GCE decreases with increasing body mass. Reiss (1989) reviewed the theoretical basis and empirical evidence for eq. 5, but there are still ambiguities in eq. 5 that deserve clarification.

Von Bertalanffy (1957) considered growth to be the difference between "anabolism" (pW^m) and "catabolism" (qW^n). Subsequent studies have interpreted growth in various ways. One is the difference between consumption and all of nongrowth components in consumption (Reiss 1989), which gives Ivlev's (1945) growth efficiency $k1$ or GCE. The second interpretation is the difference between assimilation and respiration (Ursin 1979), which may relate to Ivlev's growth efficiency $k2$ or net conversion efficiency (NCE = growth/assimilation, where assimilation = consumption – egestion – excretion). The third interpretation for growth is the difference between tissue synthesis and tissue turnover (Houlihan et al. 1992), so we have Ivlev's growth efficiency $k3$ (growth/production, where production = assimilation + tissue turnover – respiration and growth = production – tissue turnover).

Ivlev (1945) introduced the important definition of production as tissue generation regardless of subsequent fate (i.e., production is non-negative), but he did not make his $k3$ concept clear (Winberg 1956; see also comments by Ricker in the 1996 English translation of Ivlev's original paper). After Ricker's (1979) extensive review, few studies have attempted to clarify energetic interpretations of growth models. In analyzing individual growth and related energy demand, the important concept of non-negative production has never been used. Consequently, von Bertalanffy's self-

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regulation ($k3$ relationship) and Winberg's energy balance ($k2$ relationship) have been incorrectly used as interchangeable models. They have been expressed by the same equation (eq. 4), and their differences and linkages have been confounded. Without applying the concept of non-negative production, Winberg's energy balance may not be complete. Without a complete energy balance, it also may be difficult to understand von Bertalanffy's organismal self-regulation.

The first of the above interpretations for growth (eq. 4) made an aggregation of egestion, excretion, and respiration. Such an aggregation is useful for evaluating trophic interactions but may confound self-regulation of an organism. A fish may increase body length as it loses its body mass. A fish also may produce gonad mass using its somatic energy. Both assimilation and endogenous energy utilization are energy flows in the metabolic system of an organism, while some parts of consumption, such as egestion and excretion, are not in the metabolic system. The second of the above interpretations for growth may not encompass the complete meaning of Ivlev's $k2$ efficiency. It regards the residual between assimilation and growth as total respiration, but that residual also includes material for tissue replacement (Pandian 1967). The third of the above interpretations ($k3$ = growth/production) does not provide a basis for estimating exogenous energy demand. Production may rely on either or both exogenous and endogenous materials.

To study mechanisms for regulating organismal growth as well as reproduction, it is important to clearly set up the system boundary, so eq. 5 (and eq. 1) may not be a correct reinterpretation of the Pütter – von Bertalanffy growth model. To make a correction, a necessary step is to extend Winberg's (1956) energy balance as follows:

$$(6) \qquad dW/Wdt = A - R - \beta(\tau) = \alpha(dC/Wdt) - R - \beta(\tau)$$

where A is specific assimilation rate ($g \cdot g^{-1} \cdot t^{-1}$ or $J \cdot J^{-1} \cdot t^{-1}$, where t is unit time), R is specific respiration rate ($g \cdot g^{-1} \cdot t^{-1}$ or $J \cdot J^{-1} \cdot t^{-1}$), τ is specific rate of tissue turnover ($g \cdot g^{-1} \cdot t^{-1}$ or $J \cdot J^{-1} \cdot t^{-1}$), α is non-dimensional assimilation efficiency (assimilation/consumption), and β is a replacement coefficient or the proportion of tissue turnover that is not recycled (endogenous excretion). A similar analysis can be seen in Jobling (1985). Unfortunately, he did not have information about the positive relationship between tissue turnover and growth. He followed von Bertalanffy in regarding tissue breakdown as a constant proportion of body mass.

If τ had been evaluated in the context of a detailed energy balance study, we would be able to build on the complex model (Kitchell et al. 1977; Stewart et al. 1983) to analyze relationships of τ with other energy components and to evaluate its effects on energy balance. In the absence of such studies, we may aggregate R and $\beta(\tau)$ and modify eqs. 5 and 1 as follows:

$$(7) \qquad NCE = 1 - aW^b$$

Although we did not change the form of equations (eqs. 5 and 7), we clarified the biological meaning of mathematical terms. Such clarifications allow us to consider a growth process including both somatic and gonadal growth. It may appear reasonable to aggregate somatic and gonadal growth as total "production," but such an aggregation needs to be done with caution. Tissue replacement ($\beta(\tau)$) is also a part of production but would be aggregated with respiration. Gonadal growth is at least partially turnover from somatic tissue to gonadal tissue but would be aggregated with somatic growth. After sexual maturity, female fish can increase gonadal percentage of total body mass from 1–3% to 10–70% in a few months, showing an exponential growth of gonadal mass (e.g., Ware and Tanasichuk 1989; Hop et al. 1995). The differences between gonadal growth and somatic growth, and their relative metabolic costs, should not be confounded.

A proper aggregation may be to consider reproduction as a part of tissue turnover. Such an aggregation would allow us to estimate energy demand based on somatic growth patterns (Pauly 1986). The parameter a in eq. 7 is related to the maximum NCE. If we use body energy rather than body mass, the maximum NCE is about 0.96 (Calow 1977; Brafield and Llewellyn 1982), so the parameter a has a theoretical value of about 0.04. At the theoretical asymptotic size, somatic NCE is zero, although gonadal growth and tissue turnover are not zero. Setting NCE equal to zero at the asymptotic body energy, we can estimate the parameter b for eq. 7 and calculate an NCE curve versus body energy (see detailed assumptions in following application section). Using that NCE curve, we must be aware that reproduction energy has been aggregated with tissue turnover for mature fish and has not been quantified explicitly.

With either of the foregoing schemes of component aggregation, we cannot use eq. 7 to address the linkages and differences between somatic and gonadal growth. The second scheme of aggregation, however, has much less conceptual ambiguity than the first one. Eventually, gonadal tissue will be lost or reabsorbed, so it is a special case of tissue turnover. From such a consideration, we may take the Pütter – von Bertalanffy model (eqs. 4 and 7) as the critical first step to developing a general growth model.

Towards a general model for growth and reproduction

A growth process includes both energy demand–supply relationships (Winberg 1956) and the self-regulation of an organism (von Bertalanffy 1957). What has been missing in energetics-based growth models is the relationship between endogenous and exogenous flows or the regulatory role of endogenous energy flow (Fig. 1). In subsequent paragraphs, we combine the Pütter – von Bertalanffy model into a general structure to address the above relationships.

At every growth step, there is a given G, a given τ, and a given NCE. These variables are all allometric functions of total body energy. At a given growth step, if an organism could grow from the existing body energy (W) to its asymptotic body energy (W_a), it would require a certain quantity of assimilation ($(W_a - W)$/NCE) and would have a certain quantity of tissue turnover, $t(\tau)W$, where t is the time required for W to produce ($W_a - W$) with its given G. Both ($W_a - W$)/NCE and $t(\tau)W$ are potential energy flows in the metabolic system under that conditional growth. The former would be exogenous, and the latter would be endogenous.

In a growth process, negative feedbacks of the increasing total body energy are the ontogenetic changes in the foregoing energetic relationships. When total body energy in-

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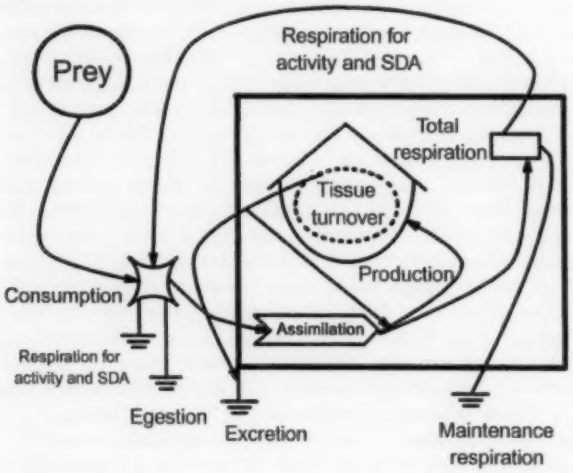
Fig. 1. Energy flows in the metabolic system of an organism, indicating production as a non-negative concept, where assimilation = consumption – egestion – excretion; production = assimilation + tissue turnover – respiration; and growth = production – tissue turnover.



creases, the ratio of τ/G increases, NCE decreases (eq. 7), and the metabolic demand ($(W_a - W)$/NCE) for producing ($W_a - W$) increases. In total respiration, the proportion of maintenance respiration including energy cost for rebuilding broken-down tissues will increase as body energy increases, and the proportion of useful activity for energy acquisition will decrease (Fig. 1). Thus, the organism must decrease its specific rate of assimilation as its total body energy increases.

The above observations and concepts can be expressed as follows:

$$(8) \quad G = (\mathrm{NCE})A$$

$$(9) \quad A = A_m(W_a - W)/[((W_a - W)/\mathrm{NCE}) + t(\tau)W]$$

where G is specific growth rate, NCE follows eq. 7, A is specific assimilation rate, and A_m is the maximum specific assimilation rate for an organism in a given environment. W_a is the body energy at infinite time when NCE is zero. When NCE equals 1 and τ equals zero, A is A_m. Both W_a and A_m are theoretical. Their empirical foundations are the above-mentioned negative allometric functions of total body energy, including NCE, specific growth rate, and specific assimilation rate. In comparison with the Monod model (Monod 1942, 1950), eq. 9 uses energetic components in a metabolic system, rather than environmental factors such as resource abundance. In comparison with the logistic model (Verhulst 1838; Pearl and Reed 1920), eq. 9 expresses potential exogenous and endogenous metabolic demand for producing ($W_a - W$), but does not regard ($W_a - W$) as "unutilized environmental capability."

Because t actually equals $(W_a - W)/GW$, eq. 9 can be rewritten as

$$(10) \quad A = A_m/((1/\mathrm{NCE}) + \tau/G)$$

Rearranging eq. 10 with eq. 8, we have

$$(11) \quad A = A_m(\mathrm{NCE}) - \tau$$

From eq. 11, we can provide further explanation of our model. There are positive empirical relationships among NCE, τ, G, and A (Houlihan and Laurent 1987; Houlihan et al. 1988, 1992). When obtaining exogenous energy is the purpose of an organism and its endogenous energy release is a necessary input or an unavoidable byproduct of that action, the above positive relationships are understandable. There must be a final constraint, however, on total energy flow in the metabolic system. That constraint is the potential tissue rebuilding ability (A_m(NCE)) of an organism because absorption of exogenous energy and mobilization of endogenous energy are similar processes. In other words, a fish could maximize its tissue mobilization according to its potential rebuilding ability, but part of its effort is always directed to acquisition of exogenous energy (eq. 11; Fig. 1). Notice that, like W_a, A_m is a theoretical potential of a fish in a given environment, rather than an observed maximum specific flux in the metabolic system. As total body energy increases, the ratio of τ/G increases (i.e., $k3$ decreases), so NCE must decrease (eq. 7). Then, for a given A_m, there will be correlated decreases in specific assimilation rate (A; eq. 10), specific growth rate (G; eq. 8), and the specific rate of tissue turnover (τ; eq. 11).

After sexual maturity, there will be gonadal growth:

$$(12) \quad G_g = A_g(\mathrm{NCE}_g)$$

where NCE_g is energy net conversion efficiency for gonadal growth, G_g is gonadal specific growth rate, and A_g is gonadal specific assimilation rate. In the relatively constant condition inside the body, gonads grow exponentially (Eschmeyer 1955; Ware and Tanasichuk 1989; Hop et al. 1995), so G_g, A_g, and NCE_g are approximately constant, at least for a fish during a given reproductive cycle. In a reproductive season, the ratio of gonadal to total body energy increases, so A_g and NCE_g must be larger than A and NCE, respectively.

Growth potential should be the same for both somatic and gonadal tissue because there is no fundamental difference between them. They have different specific growth rates because endogenous energy demand for gonadal growth draws on somatic tissue. Under the conditions where gonadal tissue is rapidly growing, the reabsorption of gonadal tissue is negligible. In contrast, the specific rate of somatic turnover will increase after sexual maturity because of the added turnover demands related to gonadal growth.

To implement the above relationships for mature fishes, we need to replace A_m(NCE) with $A_m(\mathrm{NCE}_g)$ in eq. 11:

$$(11a) \quad A = A_m(\mathrm{NCE}_g) - \tau$$

and express gonadal specific assimilation rate as a special case of eq. 11*a*:

$$(13) \quad A_g = A_m(\mathrm{NCE}_g)$$

Notice that A is specific assimilation rate for the whole body, and *NCE* in eqs. 7 and 8 treats energy for reproduction as a part of the "cost" component. Independently, eqs. 12 and 13 treat gonadal tissue as a subsystem. That subsystem can simply use somatic energy whenever necessary, so A_gW_g

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can be a part of AW or a part of τW, where W_g is gonadal energy (J). If we use NCE rather than NCE_g in eq. 13 and do not distinguish eqs. 11 and 11*a*, simulated gonadal growth will be too slow for old age-classes.

In addition to the direct energy demand for gonadal growth (eqs. 12 and 13), the effect of gonadal growth on somatic tissue is also expressed in eq. 11*a*. In this study, we can estimate energy assimilation based on observed growth using eq. 7. Then, with a consistent decreasing trend of specific assimilation rate versus total body energy, the difference between eqs. 11 and 11*a* implies a relative increase in the specific rate of tissue turnover after sexual maturity, rather than increases in specific rates of assimilation or growth. We suggest that the value of NCE_g results from adaptation of a fish to a given environment. A high NCE_g can lead to high reproductive effort (eqs. 12 and 13) but that usually involves high mortality risk (Gunderson 1997). Our model suggests that natural mortality related to energetic constraints can be quantified based on the specific rate of tissue turnover. Those additional contexts, however, will not be presented in this paper.

Some fish do not have exogenous assimilation during reproduction. Their reproduction fully relies on turnover of somatic tissue, so $A_g = \tau$ when A equals zero (eqs. 11*a* and 13). Somatic tissue is larger than gonadal tissue, so somatic tissue turnover will provide energy for respiration. The equivalence of A_g and τ reflects our inference that absorption of energy and mobilization of body energy are similar processes. The average specific flux in somatic tissue is the same as in gonadal tissue, but energy partitioning within those two compartments differs. The former includes energy transformation to gonadal tissue, necessary rebuilding of somatic tissue or metabolic substances, and somatic respiration. The latter only includes gonadal growth and respiration.

If resource abundance is very low and somatic storage is very poor, a fish may fail to reproduce even after sexual maturity (Trippel and Harvey 1989; Henderson et al. 1996), or a considerable proportion of an ovary may fail to ripen. Those phenomena result from temporal, spatial, and individual variations in A_m and NCE_g. After reproductive season or when a fish stops gonadal growth, gonadal tissue can be considered a form of somatic storage; thus, its reabsorption may follow eq. 11. Those details are also beyond the scope of this paper (but see a slightly different treatment by Van Winkle et al. 1997).

Energy acquisition by lake trout in Lake Michigan: comparisons between two models

In this section, we apply eqs. 7–13 to estimate energy assimilation of a lake trout in Lake Michigan and compare our results with those from a more complex model (Stewart et al. 1983). Both models are expansions of the Pütter – von Bertalanffy model. To improve our biological understanding, it is interesting to analyze reasons why the two models can or cannot give similar results.

Estimates from the model of Stewart et al. (1983)

The Stewart et al. (1983) model is one of the most comprehensive energetic models for fishes (Hewett and Johnson 1992; Gerking 1994; Hanson et al. 1997). The framework of the complex model has been continuously used for evaluating salmonine stocking rates and prey fish production in the Laurentian Great Lakes (Stewart et al. 1981; Stewart and Binkowski 1986; Brandt et al. 1991; Stewart and Ibarra 1991; Lantry and Stewart 1993; Negus 1995; Rand et al. 1995; Rudstam 1996; Rand and Stewart 1998). The basic model structure also has been applied to estimate consumption by various salmonines in the Pacific Northwest, and model estimates have compared favorably with independent field estimates (Beauchamp et al. 1989; Brodeur et al. 1992). Such comparative analyses, however, require catching and sacrificing large numbers of individuals for a single daily consumption estimate. That requirement so far has precluded testing the lake trout model of Stewart et al. (1983) against independent field estimates of consumption.

To facilitate comparisons between models, we summarized the complex model in Table 1, and a general discussion about the model structure has been given in a previous section. We retained the same site-specific variables such as temperature regime, prey composition, and prey energy density that were applied in Stewart et al. (1983, p. 689 and Table 2). We updated the model based on new information on lake trout body size at ages (Keller et al. 1990).

The model was run on a daily time scale, and we summarized modeling results on a yearly basis (Table 2). Stewart et al. (1983) provided an explicit treatment of energy flow and conversion. For their practical application, however, they only reported mass growth and consumption. They also expressed GCE as mass conversion efficiency. In this paper, to compare the modeling results with that from our new model, we used the specific rates of energy assimilation and energy growth ($J \cdot J^{-1} \cdot t^{-1}$; Table 2). The assimilation efficiency and NCE were expressed as energy efficiencies. Stewart et al. (1983) treated gonadal growth and somatic growth as the same process. Such a treatment does not allow gonadal percentage to increase within a given reproductive season. At spawning time, however, 6.8% of total body energy was reduced as reproductive loss (Stewart et al. 1983). To compare results from the 1983 model with those estimated by eq. 7, the calculated energy NCE excludes gametes from observed growth (Table 2).

Estimating energy assimilation using eq. 7

Using only two parameters, eq. 7 allows us to estimate the pattern of specific assimilation rate ($J \cdot J^{-1} \cdot year^{-1}$) based on a pattern of specific growth rate. From parameters for the von Bertalanffy growth curve and the length–mass relationship presented in Keller et al. (1990) and mass–energy relationships in Table 1, we calculated W_∞ as 129.15×10^6 J. Following Calow (1977), we set the parameter a in eq. 7 equal to 0.04, assuming that an extremely small fish with only 1 J of body energy has the theoretical maximum NCE value of 0.96. In fish early life history, there may be an initial stage where NCE increases with increasing body size (He 1996). Here, the theoretical maximum value is used for understanding the decreasing trend of NCE versus body size, which is typical of fishes beyond that initial stage.

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Table 1. Lake trout bioenergetics model of Stewart et al. (1983).

(A) The specific rate of consumption (C, g·g^{-1}·day^{-1}) is a function of body mass (W, g), temperature (T), and food availability (P):

$$C = 0.059W^{-0.307}e^{0.123TP}$$

(B) The proportion of egestion (F) to consumption is a function of temperature and food availability, but it needs to be adjusted for food composition:

$$F/C = [(0.212T^{-0.222}\ e^{0.631P} - K_{inv})(1 - K)/(1 - K_{inv})] + K$$

$$K = (P_{inv}K_{inv}) + (1 - P_{inv})K_{fish}$$

where $K_{inv} = 0.10$ is indigestible proportion of an invertebrate diet, $K_{fish} = 0.033$ is indigestible proportion of a fish diet, and P_{inv} is the invertebrate proportion of food.

(C) The proportion of excretion (E) to ($C - F$) is also a function of temperature and food availability:

$$E/(C - F) = 0.0314T^{0.580}e^{-0.299P}$$

(D) The specific dynamic action (SDA) is a constant proportion of ($C - F$):

$$SDA = 0.17(C - F)$$

(E) The specific rate of respiration (excluding SDA) in terms of prey biomass (R, g·g^{-1}·day^{-1}) is a function of lake trout body mass, temperature, and swimming speed (U, cm·s^{-1}); the swimming speed in turn is a function of body mass and temperature:

$$R = 0.004\,63\ (Q_{O_2}/Q_{prey})W^{-0.295}e^{0.059T}e^{0.0232U}$$

$$U = 11.7W^{0.05}e^{0.0405T}$$

$$Q_{O_2} = 13\,560$$

$$Q_{prey} = f(\text{time})$$

where, Q_{O_2} is energy value of oxygen (J·g O_2^{-1}) and Q_{prey} is energy density of prey (J·g^{-1}), which may change through time.

(F) The specific rate of growth (G) is adjusted by prey and predator energy density (for practical operation, see Stewart et al. 1983, eqs. 16–19):

$$G = [(C - F - E) - (SDA + R)]Q_{prey}/Q_{pred}$$

$$Q_{pred} = 5700 + 3.08W, \text{ when } W \leq 1472 \text{ g}$$

$$Q_{pred} = 9090 + 0.778W, \text{ when } W > 1472 \text{ g}$$

Table 2. Growth of average individual lake trout in Lake Michigan and modeled energetics using the model of Stewart et al. (1983).

Age-class	Initial body mass (g)	Gametes lost (g)	Initial body energy (J, ×10^6)	Specific rate of assimilation (J·J^{-1}·year^{-1})	α	Specific rate of growth (J·J^{-1}·year^{-1})	NCE	P
1	30.7		0.18	18.35	0.76	6.75	0.368	0.6543
2	216.7		1.38	6.30	0.78	2.26	0.360	0.5604
3	597.8		4.51	3.51	0.79	1.32	0.378	0.5700
4	1138.7		10.48	2.13	0.79	0.78	0.367	0.5459
5	1781.4		18.66	1.44	0.80	0.46	0.318	0.4905
6	2470.2	192.6	27.20	1.28	0.79	0.34	0.268	0.5216
7	3160.9	240.4	36.51	1.08	0.79	0.26	0.244	0.5092
8	3822.7	285.4	46.12	0.95	0.80	0.21	0.217	0.4997
9	4436.3	327.0	55.64	0.84	0.80	0.16	0.195	0.4903
10	4991.7	364.0	64.76	0.77	0.80	0.13	0.171	0.4815

Note: Body mass is the initial body mass of each age-class on July 1. For mature fish, average gametes lost for both sexes is 6.8% of total body mass and is treated as a step function on October 30. Age-class 0 is not included because virtually all lake trout in Lake Michigan are of hatchery origin and stocked at age 1. α, Assimilation efficiency (assimilation/consumption); NCE, energy net conversion efficiency (growth/assimilation), where to compare with estimates from eq. 7, growth does not include gametes lost; P, ratio of estimated specific rate of consumption to the specific rate of consumption when food is unlimited.

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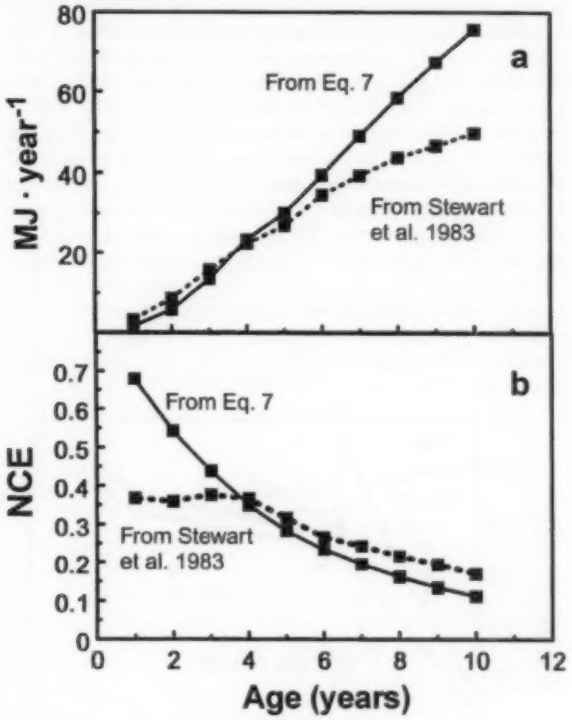
Fig. 2. (*a*) Comparisons between two model estimates of energy assimilation for a lake trout growing from the start of age-1 to the end of age-10. The estimates are for both somatic and gonadal growth when a fish is mature (age-6 and older). (*b*) Comparisons between two model estimates of energy net conversion efficiency (NCE = growth/assimilation; growth did not include gametes lost).



Calow's (1977) theoretical calculation has rarely been applied in practical studies. We found that when we use body energy (J) rather than body mass, eq. 7 with Calow's maximum NCE value provided a reasonable estimation of NCE pattern versus body energy. With a equal to 0.04 and setting NCE equal to zero at the asymptotic body energy (129.15×10^6 J), we solved for the parameter b = 0.1723 in eq. 7. Then, a 1-year-old lake trout, with 30.7 g body mass and 0.18×10^6 J body energy, has a NCE value of 0.679. Lake trout energy density was higher than its prey energy density, and the invertebrate diet of age-1+ lake trout leads to a lower assimilation efficiency than that of older age-classes feeding on fish (Stewart et al. 1983). Thus, mass NCE at age-1 will be less than 50%, and mass GCE at age-1 will be around 35%.

From body energy at ages, we calculated the specific rate of growth ($J \cdot J^{-1} \cdot \tau^{-1}$) for each age-class (Table 2). Using eq. 7 with the above-estimated parameter values, we calculated specific assimilation rate (assimilation = growth/NCE). For immature lake trout growing from the initial size of age 1 to the final size of age-5, the estimated total assimilation (MJ) from eq. 7 was 3.1% less than that from the complex model (Fig. 2*a*). For mature lake trout growing from the initial size of age-6 to the final size of age-10, the estimated total assimilation from eq. 7 was 35.4% higher than that from the complex model (Fig. 2*a*). For the whole process of 10 years of growth, the estimated total assimilation from eq. 7 was 25.3% higher than that from the complex model.

When empirical growth pattern and energy density were given, the results from eq. 7 depended on the value of parameter a. A 10% increase or decrease in the value of parameter a did not change the general results. The estimated total energy assimilation from eq. 7 was about 21.7–28.7% higher than that from the complex model. From the complex model, assimilation efficiency (α) of food energy had a range of 0.76–0.80 (Table 2); those values can be used to calculate consumption (consumption = assimilation/α) for each age-class. For our new model, assuming an assimilation efficiency of 0.80 (Winberg 1956) yielded total consumption estimates that were also about 25% higher than the complex model.

Do reproduction costs explain differences between model estimates?

Using eqs. 7–13, we may evaluate the effect of gonadal growth on total energy assimilation. First, we need to estimate the maximum specific rate of assimilation (A_m). Notice that in the complex model (Table 1), the maximum specific rate of consumption was defined as the specific consumption rate of any given-sized individual when food is unlimited. For our new model, the maximum specific assimilation rate (A_m) is defined such that, in a given environment, specific assimilation rate decreases as body energy increases. From eqs. 9–11, when NCE equals 1 and tissue turnover equals 0, A equals A_m. Considering that both NCE and specific assimilation rate decrease as body energy increases, we can plot the estimated specific assimilation rate versus NCE and extrapolate that relationship to estimate the theoretical maximum value A_m (Fig. 3). The estimated A_m was 34.39 ($J \cdot J^{-1} \cdot year^{-1}$).

Then, on a daily scale, we used eqs. 7 and 8 to simulate somatic growth and eqs. 12 and 13 to simulate gonadal growth (Fig. 4). Eschmeyer (1955) reported that average gonadal percentage of total body mass was 12.3% for lake trout females. The pattern of somatic growth is also known (Table 2), so the above simulation allowed us to estimate NCE_g for gonadal growth. Our simulation for an age-6 lake trout (first age of more than 50% maturity) suggested that reaching a gonadal energy of 12.3% total body energy requires an NCE_g of 0.270. A 10% decrease or increase in the estimated NCE_g value yielded gonadal percentages of 9.2 and 16.8%, respectively. A 10% decrease or increase in A_m produced gonadal percentages of 10.6 and 14.3%, respectively. With NCE_g equal to 0.270 and A_m equal to 34.39, an age-10 female lake trout will have a gonadal percentage of 13.8%. All of those estimated values fall within the range of empirical observations (Eschmeyer 1955). In contrast to females, males have a small gonadal percentage and a short gonadal development period (Eschmeyer 1955). We assumed that lake trout males have NCE_g values similar as those for females.

Based on eq. 7 and related parameter values, the estimated NCE values for mature lake trout (age-6 to age-10) were 0.235–0.112 (Fig. 2). Based on the daily scale simulation for both somatic growth (eqs. 7 and 8) and gonadal growth

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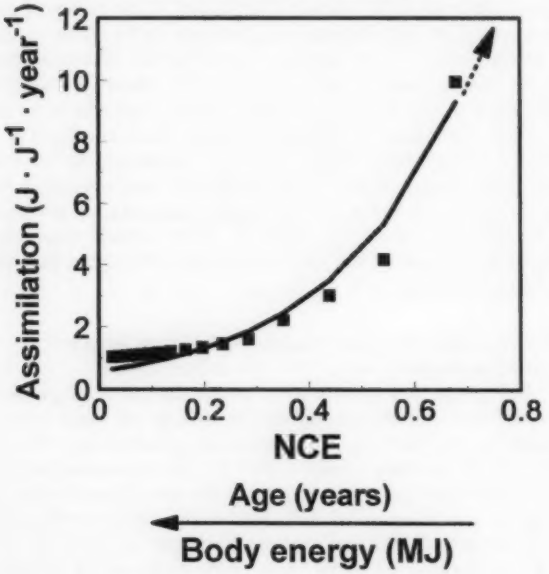
Fig. 3. Estimating the maximum specific assimilation rate based on the trends of NCE and specific assimilation rate as age or body energy change. $A = 0.5821e^{4.0788NCE}$ ($R^2 = 0.98$), so A_m equals 34.39 $J \cdot J^{-1} \cdot year^{-1}$ when NCE equals 1.0. Regression was done using a nonlinear procedure (SAS Institute Inc. 1992).



(eqs. 12 and 13), the exponential growth of gonadal tissue required a nearly constant NCE_g (0.270). Many empirical comparisons between gonadal and somatic growth efficiencies provided similar results (Brody 1945; Wootton and Evans 1976; Calow 1983; Rogers 1988). When gonadal growth is more efficient than adult somatic growth, we cannot use the direct cost of gonadal growth to explain the differences in estimated total energy assimilation between eq. 7 and the model of Stewart et al. (1983), although the latter model regarded gonadal and somatic growth as equivalent processes.

The primary difference between the two models and implications for future studies

There have been studies suggesting that the commonly used fish energetic models may underestimate consumption (Boisclair and Leggett 1989), particularly for mature fishes (Rowan and Rasmussen 1996). Their focus and energetic implications were different from our modeling analysis. For example, Rowan and Rasmussen (1996) suggested that activity can increase respiration of mature lake trout to as high as 4.19–6.97 times basal respiration. Using those estimates of activity costs and the swimming speed model of Stewart et al. (1983), mature female lake trout in lakes would be swimming 62–84 cm/s 24 h per day. In comparison, 3+ kg coho salmon (*Oncorhynchus kisutch*) and 5+ kg steelhead trout (*O. mykiss*) in the Pacific Ocean typically swim less than 45 cm/s (Ruggerone et al. 1990; Ogura and Ishida 1992; Rand et al. 1993).

The term of activity has been widely used without a clear definition. It is often calculated as (assimilation – growth – basal respiration)/basal respiration (Rowan and Rasmussen 1996), but the result has been referred to as swimming or mechanical activity. Special care must be taken as follows:

(1) Basal respiration is temperature dependent. Using the complex model to calculate activity must specify the temperature that has been used for calculating basal respiration.

(2) When assimilation or consumption is estimated based on the specific rate of growth, the conceptual basis for the calculation also must be specified. In Stewart et al. (1983) and Rowan and Rasmussen (1996), gonadal growth was actually treated as energy or mass transformation from somatic tissue to gonadal tissue with an implied efficiency of nearly 100% (i.e., loss of somatic tissue to gonadal tissue without metabolic cost). Such an treatment may lead to an overestimate of energy demand in Rowan and Rasmussen's approach (He and Stewart 1997) and leave ambiguities in the complex model framework.

Fig. 4. Simulated daily somatic and gonadal growth of an age-6 lake trout based on our new model. The simulation was for 1 year. Initial and final body energy were calculated from empirical data (Stewart et al. 1983; Keller et al. 1990). Somatic growth follows eq. 8, and NCE for somatic growth follows eq. 7 ($a = 0.04$, $b = 0.1723$). The specific assimilation rate (A, $J \cdot J^{-1} \cdot year^{-1}$) was calculated from empirical annual specific growth rate (Table 2) and NCE, but the value of A was transformed to daily scale values ($J \cdot J^{-1} \cdot year^{-1}$) according to the following seasonal distribution: 70% in July to October; 15% in November to April; and 15% in May to June (Fry 1952; Lawrie 1963; Eck and Wells 1986). For this simulation, we did not consider fine details of daily temperature effect. Gonadal growth follows eqs. 12 and 13. The maximum annual specific rate of assimilation was estimated as 34.39 $J \cdot J^{-1} \cdot year^{-1}$ (Fig. 3), but that value was also transformed to daily scale values according the above seasonal distribution. We adjusted the value of NCE_g for gonadal growth until our model predicted average female gonad percentage of 3% on July 1 and 12.3% on October 31. The gonadal growth pattern follows Eschmeyer's (1955) field observations, and the model simulation treated reproduction as a step function on October 31. The estimated NCE_g for gonadal growth was 0.270.

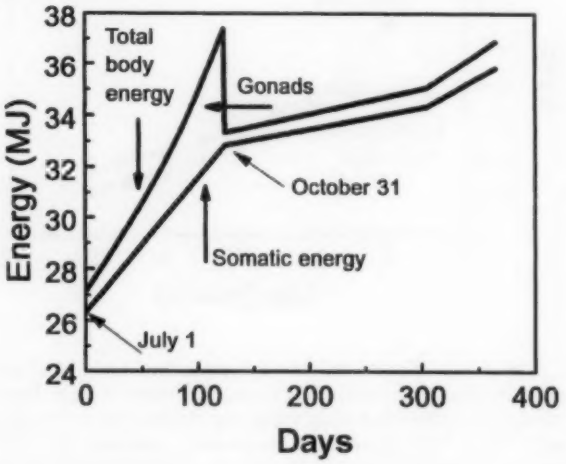


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Fig. 5. (*a*) Modeled specific rate of tissue turnover as function of body energy, with emphasis on immature lake trout (age-1to age-5; eq. 11). (*b*) Modeled specific rate of tissue turnover for mature lake trout (age-6 to age-10; eq. 11*a*).

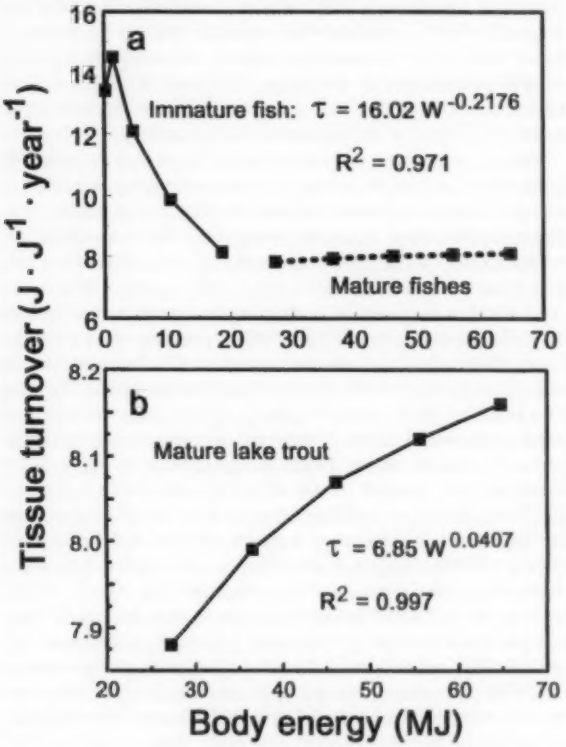
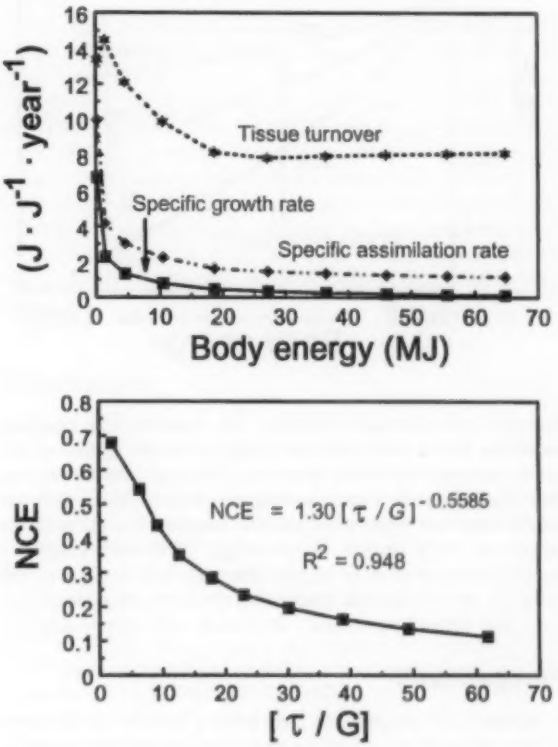


Fig. 6. (*a*) As body energy increases, specific rates of growth (*G*), assimilation (*A*), and tissue turnover (τ) decrease. The relationships among *G*, *A*, and τ are positive. (*b*) As modeled ratio of tissue turnover (τ) to growth (*G*) increases, NCE decreases.



(3) If tissue turnover increases with somatic or gonadal growth, related energetic cost should not be vaguely covered using mechanical activity.

A fish can have a higher specific assimilation rate for gonadal tissue than for somatic tissue, and our new model provided an explicit treatment. In addition to the direct energy demand for gonadal growth (eqs. 12 and 13), the rapid growth of gonadal tissue leads to increases in specific rate of somatic tissue turnover (eqs. 11 and 11*a*). For immature age-classes (age-classes 1–5), the estimated specific rate of tissue turnover followed a simple negative power function, except that age-class 1 somehow appeared to have different behavior (Fig. 5*a*). In an experimental study on rainbow trout, Houlihan et al. (1986) found a similar relationship, but their observations were based on body mass and protein turnover rather than total body energy and energy turnover. For sexually mature fishes, no experimental observations are available for comparison. Our model simulation suggested that, from age-6 to age-10, the specific rate of tissue turnover was relatively stable (Fig. 5*a*). On closer examination, however, the specific rate of tissue turnover increased slowly with total body energy, following a positive power function (Fig. 5*b*). Based on eqs. 7–11*a*, the modeled relationships among specific rates of growth, assimilation, and tissue turnover are positive (Fig. 6*a*). As the modeled ratio of tissue turnover to growth increases, NCE decreases (Fig. 6*b*). Those relationships are consistent with empirical observations cited repeatedly in previous sections and were the basis for our model structure. Notice that the structural developments of eqs. 7 and 11 are independent of one another.

We cannot add the above-estimated tissue turnover as an new energy component in the energy balance of the complex model. As we indicated in previous sections, there are complex relationships among tissue turnover and other energetic components. The energy loss or cost related to tissue turnover may be partially covered by other energy components as formulated in the complex model. Our modeling results suggested that the important interrelationships of tissue turnover with other energetic components deserve explicit consideration in future studies.

The primary difference between the two models is the NCE pattern versus body energy (Fig. 2*b*). The complex model suggested NCE values with a relatively small range of variation (0.171–0.377). It also suggested that food availability (*P* value, Table 2) decreases as body size increases. Equation 7 does not involve any assumption about food availability related to age or body size. As age increases from 1 to 10 and body energy increases from 0.18 to 64.76 MJ, eq. 7 implied that NCE decreases from 0.679 to 0.112. From eq. 6, we understand that eq. 7 covers potential energy

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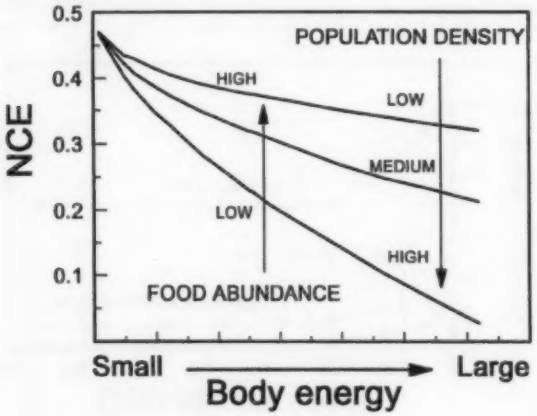
Fig. 7. Qualitative relationships among food abundance, population density, body energy, and energy net conversion efficiency (NCE).



loss or cost of tissue turnover. In contrast, the complex model included many detailed components but lacked an explicit treatment of tissue turnover. The new model implied that rapid growth must accompany higher NCE, but the model does not explicitly consider seasonal variation in the pattern of NCE versus body energy. That may lead to a slight overestimation of energy demand. Advantages of the complex model include treatments of daily temperature regime and related seasonality of growth and energy density.

Perspectives

Normally, it is relatively easy to fit a growth curve, but it is very difficult to quantify energy demand–supply relationships and to confirm or explain a regulatory mechanism (Paloheimo and Dickie 1965; Ricker 1979). Field estimates of fish consumption also require modeling processes (Bajkov 1935; Eggers 1977; Elliott and Persson 1978), so few energetic models have been really confirmed (Boisclair and Leggett 1989). To improve that situation, there have been continuing efforts to independently analyze detailed energetic components in experiments or field studies. In conjunction with those studies, our effort addresses overall structures of models as foundations for designing various empirical investigations.

Ware (1982) suggested that food consumption was a function of swimming speed. Kerr (1982) suggested that activity was a function of consumption. Those two investigators used different cause–effect relationships, although both of them were discussing similar phenomena in field or laboratory populations. The commonly used complex model used a different approach. Its flexibility in practical applications has relied on the P value (Rice and Cochran 1984; Boisclair and Leggett 1989), which is normally explained as food availability or ecological constraint on feeding level. When we force a model to fit an empirical growth curve, the P value shows either an increasing or decreasing trend versus age or body energy (Table 2; see also Stewart et al. 1983; Rudstam et al. 1994). Such regular trends have not been clearly explained.

The relationship between consumption and swimming activity may never be explainable in terms of cause and effect. The relationships of SDA to consumption, food composition, body mass, temperature, and activity are even more complex (Beamish and Trippel 1990; Krohn et al.1997). Beamish and Trippel (1990) cautioned that modelers should be aware of those real-world complexities and not oversimplify by using simple proportions or constants. We hope that interactions between modeling analyses and empirical investigations ultimately will lead to fundamental understanding.

Various energetic components are related to each other. To understand an integrative regulatory mechanism, we need to identify a key component and its relationships to others. Traditionally, the most important component has been chosen as consumption. With zero consumption, organisms have endogenous excretion and lose their body energy. With overconsumption, organisms will increase egestion and reduce assimilation efficiency (Elliott 1976). Feeding is an essential factor that influences swimming state of a fish; swimming activities, in turn, will require more consumption. Feeding also leads to SDA. From Winberg (1956), Ivlev (1961), and Paloheimo and Dickie (1965) to ongoing concerns about complex models (Kerr 1982; Boisclair and Leggett 1989; Beamish and Trippel 1990; Boisclair 1993; Krohn et al. 1997), consumption has been regarded as the most important driving factor in an energy balance system. Paloheimo and Dickie (1965) suggested that energy conversion efficiency decreases with increasing consumption rate ($g \cdot r^{-1}$). After their work, no other integrative mechanism has been suggested. Ware's (1982) work may represent a different approach. His model uses swimming speed as the central factor for optimizing energy acquisition and metabolic cost, but his energy-balance model does not address the allometry of consumption versus increasing body size.

Our new model provides an alternative perspective by emphasizing ontogeny of energetic relationships inside the metabolic system of an organism. We regard tissue turnover as the central factor. The specific rate of tissue turnover is a function of body size and various physiological states such as resting, swimming, growth, and reproduction. Basal metabolism is related to minimum rebuilding of tissues or metabolic substances. The cost of swimming, energy acquisition, and growth includes the increases in maintenance demand due to increases in tissue turnover.

On one hand, the specific rate of tissue turnover is positively related to NCE and various activities mentioned above. On the other hand, an increase in the ratio of tissue turnover to growth is responsible for the ontogenetic decreases in NCE and specific rates of assimilation and growth. Thus, endogenous energy flow plays a regular role for living activities. Certainly, there will be dynamic linkages between environmental changes and those ontogenetic processes. With low food abundance and high population density, endogenous demand will be high for acquiring exogenous energy, and NCE will decrease rapidly with increasing body size (Fig. 7). We leave more detailed discussions to subsequent developments and applications.

The Pütter – von Bertalanffy model has been widely used in both theoretical and empirical studies (Ricker 1975, Beverton and Holt 1993). It is good for fitting and comparing growth data, but its energetic basis has never been made

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clear (Ricker 1979). It was originally based on mass-balance considerations (von Bertalanffy 1957) and has been the basis for various complex energetic models (e.g., Kitchell et al. 1977; Stewart et al. 1983). The Pütter – von Bertalanffy growth model, however, has rarely been used for quantifying energy demand–supply relationships. Following Brett (1970), Ursin (1979), Pauly (1986), and Reiss (1989), we show that the Pütter – von Bertalanffy model expresses a decreasing trend in NCE versus body energy, but the model structure does not express a mechanism for regulating ontogenetic changes in energy acquisition.

Our new model embodies an integration of fundamental concepts from the Pütter – von Bertalanffy, the Monod and the logistic models. The model structure includes three allometric functions of total body energy: growth, assimilation, and tissue turnover. The last one is the endogenous energy flow and may play a regulatory role when an organism responds to various environmental factors. Once those allometric functions have been independently quantified in a given experimental setting, we can use their relationships to exactly evaluate our model structure (eqs. 7–13). The model structure is analogous to the Monod model, so we may have a basis for studying the linkages between environmental controls and organismal responses. In analogy to the logistic model (see Ricker 1979), our model uses the W_a and A_m. The former is the body energy where NCE equals zero. The latter is the maximum specific assimilation rate when NCE equals 1 and specific rate of tissue turnover equals zero. Both W_a and A_m are theoretical, but both of them are implied by empirical patterns of NCE, specific assimilation rate, and specific growth rate versus body energy. The linkage between W_a and A_m is NCE, which is expressed by the Pütter – von Bertalanffy growth function (eqs. 4 and 7). Those relationships allow us to quantify parameter values when growth patterns are the only available data. Thus, our model is operational for practical applications.

Previous studies towards energetics-based population dynamic models include Ursin (1967), Van Winkle et al. (1997), and Jensen (1998). Using our new model we can address general regulatory mechanisms and provide an energetic framework for combining individual growth and reproduction. Such a linkage is essential for applications to population and food web dynamics. To emphasize integrative feedback structures (eqs. 9–11; Fig. 1), we reduced the complex expansion of the Pütter – von Bertalanffy model (Stewart et al. 1983) to its simplest form (NCE; eq. 7). Future experimental studies may provide a basis for including tissue turnover in the framework of the complex model. That, in turn, may allow us to abandon the use of P values to force a model to fit observed growth. In future developments and applications, it may be useful to expand our NCE equation to encompass much of the complex model with tissue turnover included. Those energetics details would allow us to apply our model on a finer time scale to evaluate dynamic effects of temperature, prey abundance, and other environmental factors. The specific rate of tissue turnover and its relationship to energetic constraints may provide a mechanistic basis for estimating natural mortality. Adding mortality due to predation and fishing will yield a complete energetics-based population dynamics model. Such a model will allow for evaluating future population trajectories in the context of food web dynamics and under various management scenarios.

Acknowledgments

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References

Adams, S.M., and Breck, J.E. 1990. Bioenergetics. *In* Methods for fish biology. *Edited by* C.B. Schreck and P.B. Moyle. American Fisheries Society, Bethesda, Md. pp. 389–415.

Ashworth, A. 1969. Metabolic rates during recovery from protein-calorie malnutrition: the need for a new concept of specific dynamic action. Nature (London), **223**: 407–409.

Bajkov, A.D. 1935. How to estimate the daily food consumption of fish under natural conditions. Trans. Am. Fish. Soc. **65**: 288–289.

Beamish, F.W.H. 1970. Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. Can. J. Zool. **48**: 1221–1228.

Beamish, F.W.H. 1974. Apparent specific dynamic action of largemouth bass, *Micropterus salmoides*. J. Fish. Res. Board Can. **31**: 1763–1769.

Beamish, F.W.H., and Trippel, E.A. 1990. Heat increment: a static or dynamic dimension in bioenergetic models. Trans. Am. Fish. Soc. **119**: 649–661.

Beauchamp, D.A., Stewart, D.J., and Thomas, G.L. 1989. Corroboration of a bioenergetics model for sockeye salmon. Trans. Am. Fish. Soc. **118**: 597–607.

Beverton, R.J.H., and Holt, S.J. 1993. On the dynamics of exploited fish populations. Facsimile reprint. Chapman & Hall, London.

Björnsson, B. 1993. Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: a laboratory study. Can. J. Fish. Aquat. Sci. **50**: 2542–2551.

Blaxter, J.H.S., and Hempel, G. 1963. The influence of egg size on herring larvae. J. Cons. Cons. Int. Explor. Mer, **28**: 211–240.

Boisclair, D. 1992. Relationship between feeding and activity rates for actively foraging juvenile brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **49**: 2566–2573.

Boisclair, D., and Leggett, W.C. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. Can. J. Fish. Aquat. Sci. **46**: 1859–1867.

Brafield, A.E., and Llewellyn M.J. 1982. Animal energetics. Blackie, London.

Brandt, S.B., Mason, D.M., Patrick, E.V., Argyle, R.L., Wells, L., Unger, P.A., and Stewart, D.J. 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. Can. J. Fish. Aquat. Sci. **48**: 894–908.

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Brandt, S.B., Mason, D.M., and Patrick, E.V. 1992. Spatially-explicit models of fish growth rate. Fisheries (Bethesda), **27**(2): 23–35.

Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. **21**: 1183–1226.

Brett, J.R. 1970. Fish—the energy cost of living. *In* Marine aquaculture. *Edited by* W.J. McNeil. Oregon State University Press, Corvallis. pp. 37–52.

Brett, J.R., and Groves, T.D.D. 1979. Physiological energetics. *In* Fish physiology. Vol. 8. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 279–352.

Brodeur, R.D., Francis, R.C., and Pearcy, W.G. 1992. Food consumption of juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) on the continental shelf off Washington and Oregon. Can. J. Fish. Aquat. Sci. **49**: 1670–1685.

Brody, S. 1945. Bioenergetics and growth with special reference to the efficiency complex in domestic animals. Reinhold Publishing Corporation, Baltimore, Md.

Brown, C.R., and Cameron, J.N. 1991*a*. The induction of specific dynamic action in channel catfish by infusion of essential amino acids. Physiol. Zool. **64**: 275–297.

Brown, C.R., and Cameron, J.N. 1991*b*. The relationship between specific dynamic action (SDA) and protein synthesis rates in the channel catfish. Physiol. Zool. **64**: 298–309.

Calow, P. 1977. Conversion efficiencies in heterotrophic organisms. Biol. Rev. Camb. Philos. Soc. **52**: 385–409.

Calow, P. 1983. Energetics of reproduction and its evolutionary implications. Biol. J. Linn. Soc. **20**: 153–165.

Clarke, G.L., Edmondson, W.T., and Ricker, W.E. 1946. Mathematical formulation of biological productivity. Ecol. Monogr. **16**: 336–337.

Diana, J.S., and Salz, R. 1990. Energy storage, growth, and maturation of yellow perch from different locations in Saginaw Bay, Michigan. Trans. Am. Fish. Soc. **119**: 976–984.

Durbin, A.G., Durbin, E.G., Verity, P.G., and Smayda, T.J. 1981. Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). Fish. Bull. U.S. **78**: 877–886.

Eck, G.W., and Wells, L. 1986. Depth distribution, diet, and overwinter growth of lake trout (*Salvelinus namaycush*) in southeastern Lake Michigan sampled in December 1981 and March 1982. J. Great Lakes Res. **12**: 263–269.

Eggers, D.M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. **34**: 290–294.

Elliott, J.M. 1976. Energy losses in the waste products of brown trout (*Salmo trutta* L.). J. Anim. Ecol. **45**: 561–580.

Elliott, J.M., and Persson, L. 1978. The estimation of daily rate of food consumption for fish. J. Anim. Ecol. **47**: 977–991.

Eschmeyer, P.H. 1955. The reproduction of lake trout in southern Lake Superior. Trans. Am. Fish. Soc. **84**: 47–74.

Flath, L.E., and Diana, J.S. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Trans. Am. Fish. Soc. **114**: 328–337.

Forseth, T., Jonsson, B., Næumann, R., and Ugedal, O. 1992. Radioisotope method for estimating food consumption by brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **49**: 1328–1335.

From, J., and Rasmussen, G. 1984. A growth model, gastric evacuation, and body composition in rainbow trout, *Salmo gairdneri* Richardson, 1836. Dana, **3**: 61–139.

Fry, F.E. 1952. The 1944 year class of lake trout in South Bay, Lake Huron. Trans. Am. Fish. Soc. **82**: 178–192.

Gerking, S.D. 1962. Production and food utilization in a population of bluegill sunfish. Ecol. Monogr. **32**: 31–78.

Gerking, S.D. 1994. Feeding ecology of fish. Academic Press, San Diego, Calif.

Goldspink, D.F., and Kelly, F.J. 1984. Protein turnover and growth in the whole body, liver and kidney of the rat from the foetus to senility. Biochem. J. **217**: 507–516.

Gunderson, D.R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Can. J. Fish. Aquat. Sci. **54**: 990–998.

Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish bioenergetics, version 3.0 edition. University of Wisconsin Sea Grant Institute, Madison.

Hawkins, A.J.S. 1985. Relationships between the synthesis and breakdown of protein, dietary absorption and turnovers of nitrogen and carbon in the blue mussel, *Mytilus edulis* L. Oecologia, **66**: 42–49.

Hawkins, A.J.S. 1991. Protein turnover: a functional appraisal. Funct. Ecol. **5**: 222–233.

Hawkins, A.J.S., Bayne, B.L., and Day, A.J. 1986. Protein turnover, physiological energetics and heterozygosity in the blue mussel, *Mytilus edulis*: the basis of variable age-specific growth. Proc. R. Soc. London B, **229**: 161–176.

He, J. 1996. Organismal production in open dynamic systems: an energetics-modeling synthesis with implications for ecosystem processes. M.S. thesis, College of Environmental Science and Forestry, State University of New York, Syracuse.

He, J., and Stewart, D.J. 1997. Comment: measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (^{137}Cs). Can. J. Fish. Aquat. Sci. **54**: 1953–1954.

Henderson, B.A., Wong, J.L., and Nepszy, S.J. 1996. Reproduction of walleye in Lake Erie: allocation of energy. Can. J. Fish. Aquat. Sci. **53**: 127–133.

Hewett, S.W., and Johnson, B.L. 1992. Fish bioenergetics model 2. Tech. Rep. No. WIS-SG-91-250. University of Wisconsin Sea Grant Institute, Madison.

Hop, H., Graham, M., and Trudeau, V.L. 1995. Spawning energetics of Arctic cod (*Boregadus saida*) in relation to seasonal development of the ovary and plasma sex steroid levels. Can. J. Fish. Aquat. Sci. **52**: 541–550.

Houlihan, D.F. 1991. Protein turnover in ectotherms and its relationships to energetics. *In* Advances in comparative and environmental physiology. Vol. 7. *Edited by* R. Gilles. Springer-Verlag, Berlin. pp. 1–43.

Houlihan, D.F., and Laurent, P. 1987. Effects of exercise training on the performance, growth, and protein turnover of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. **44**: 1614–1621.

Houlihan, D.F., McMillan, D.N., and Laurent, P. 1986. Growth rates, protein synthesis, and protein degradation rates in rainbow trout: effects of body size. Physiol. Zool. **59**: 482–493.

Houlihan, D.F., Hall, S.J., Gray, C., and Noble, B.S. 1988. Growth rates and protein turnover in Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Sci. **45**: 951–964.

Houlihan, D.F., Wieser, W., Foster, A., and Brechin, J. 1992. In vivo protein synthesis rates in larval nase (*Chondrostoma nasus* L.). Can. J. Zool. **70**: 2436–2440.

Ivlev, V.S. 1945. [The biological productivity of waters.] Usp. Sovrem. Biol. **19**: 98–120. (Translated from the Russian by Fish. Res. Board Can. Transl. Ser. No. 394, 1966.)

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Conn.

© 1998 NRC Canada

Jayaram, M.G., and Beamish, F.W.H. 1992. Influence of dietary protein and lipid on nitrogen and energy losses in lake trout, *Salvelinus namaycush*. Can. J. Fish. Aquat. Sci. **49**: 2267–2272.

Jensen, A.L. 1998. Simulation of relations among fish life history parameters with a bioenergetics-based population model. Can. J. Fish. Aquat. Sci. **55**: 353–357.

Jobling, M. 1981. The influences of feeding on the metabolic rate of fishes: a short review. J. Fish Biol. **18**: 385–400.

Jobling, M. 1983. Towards an explanation of specific dynamic action (SDA). J. Fish Biol. **23**: 549–555.

Jobling, M. 1985. Growth. *In* Fish energetics, new perspectives. *Edited by* P. Tytler and P. Calow. Johns Hopkins University Press, Baltimore, Md. pp. 213–230.

Keller, M., Smith, K.D., and Rybicki, R.W. (*Editors*). 1990. Review of salmon and trout management in Lake Michigan. Fish. Spec. Rep. No. 14. Michigan Department of Natural Resources, East Lansing.

Kerr, S.R. 1982. Estimating the energy budgets for actively predatory fishes. Can. J. Fish. Aquat. Sci. **39**: 371–379.

Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1922–1935.

Krohn, M., Reidy, S., and Kerr, S. 1997. Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 113–121.

Lantry, B.F., and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. Trans. Am. Fish. Soc. **122**: 951–976.

Lawrie, A.H. 1963. Intraseasonal growth in Lake Superior lake trout. J. Fish. Res. Board Can. **20**: 491–496.

Madon, S.P., and Culver, D.A. 1993. Bioenergetics model for larval and juvenile walleyes: an in situ approach with experimental ponds. Trans. Am. Fish. Soc. **122**: 797–813.

Majkowski, J., and Hearn, W.S. 1984. Comparison of three methods for estimating the food intake of a fish. Can. J. Fish. Aquat. Sci. **41**: 212–215.

Mann, K.H. 1965. Energy transformations by a population of fish in the River Thames. J. Anim. Ecol. **34**: 253–275.

McCarthy, L.D., Houlihan, D.F., and Carter, C.G. 1994. Individual variation in protein turnover and growth efficiency in rainbow trout, *Oncorhynchus mykiss* (Walbaum). Proc. R. Soc. London B, **257**: 141–147.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**: 1657–1670.

Monod, J. 1942. Recherches sur la croissance des cultures bacteriennes. Hermann & Cie, Paris.

Monod, J. 1950. La technique de culture continue: théorie et applications. Ann. Inst. Pasteur Paris, **79**: 390–410.

Muir, B.S., and Niimi, A.J. 1972. Oxygen consumption of the euryhaline fish aholehole (*Kuhlia sandvicensis*) with reference to salinity, swimming, and food consumption. J. Fish. Res. Board Can. **29**: 67–77.

Negus, M.T. 1995. Bioenergetics modeling as a salmonine management tool applied to Minnesota waters of Lake Superior. N. Am. J. Fish. Manage. **15**: 60–78.

Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand–supply relationships between predators and prey. Aquat. Sci. **2**: 55–81.

Ogura, M., and Ishida, Y. 1992. Swimming behavior of coho salmon (*Oncorhynchus kisutch*) in the open sea as determined by ultrasonic telemetry. Can. J. Fish. Aquat. Sci. **49**: 453–457.

Paloheimo, J.E., and Dickie, L.M. 1965. Food and growth of fishes. I. A growth curve derived from experimental data. J. Fish. Res. Board Can. **22**: 521–542.

Pandian, T.J. 1967. Intake, digestion, absorption and conversion of food in the fishes *Megalops cyprinoides* and *Ophiocephalus striatus*. Mar. Biol. **1**: 16–32.

Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. Fish. Bull. U.S. **84**: 827–839.

Pearl, R., and Reed, L.J. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Natl. Acad. Sci. U.S.A. **6**: 275–288.

Pütter, A. 1920. Studien über physiologische Ähnlichkeit, VI. Wachstumsähnlichkeiten. Pflügers Arch. Gesamte Physiol. Menschen Tiere, **180**: 298–340.

Rand, P.S., and Stewart, D.J. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. Can. J. Fish. Aquat. Sci. **55**: 318–327.

Rand, P.S., Stewart, D.J., Seelbach, P.W., Jones, M.L., and Wedge, L.R. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Trans. Am. Fish. Soc. **122**: 977–1001.

Rand, P.S., Stewart, D.J., Lantry, B.F., Rudstam, L.G., Johannsson, O.E., Goyke, A.P., Brandt, S.B., O'Gorman, R., and Eck, G.W. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. **52**: 1546–1563.

Rao, G.M.M. 1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. Can. J. Zool. **46**: 781–786.

Reiss, M.J. 1989. The allometry of growth and reproduction. Cambridge University Press, Cambridge, England.

Rice, J.A., and Cochran, P.A. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology, **63**: 732–739.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Ricker, W.E. 1979. Growth rate and models. *In* Fish physiology. Vol. 8. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 677–743.

Rogers, S.I. 1988. Reproductive effort and efficiency in the female common goby, *Pomatoschistus microps* (Kroyer) (Teleostei: Gobioidei). J. Fish Biol. **33**: 109–119.

Rowan, D.J., and Rasmussen, J.B. 1996. Measuring the bioenergetic cost of fish activity in situ using a globally dispersed radiotracer (^{137}Cs). Can. J. Fish. Aquat. Sci. **53**: 734–745.

Rudstam, L. (*Editor*). 1996. A review of the current status of lake Ontario's pelagic fish community. Report of the 1996 Lake Ontario technical panel. Great Lakes Res. Rev. **2**(2): 4–10.

Rudstam, L.G., Binkowski, F.P., and Miller, M.A. 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. Trans. Am. Fish. Soc. **123**: 344–357.

Ruggerone, G.T., Quinn, T.P., McGregor, I.A., and Wilkinson, T.D. 1990. Horizontal and vertical movements of adult steelhead trout, *Oncorhynchus mykiss*, in the Dead and Fisher Channels, British Columbia. Can. J. Fish. Aquat. Sci. **47**: 1963–1969.

SAS Institute Inc. 1992. The SAS system for Windows 3.10, release 6.08 edition. SAS Institute Inc., Cary, N.C.

Silvert, W., and Pauly, D. 1987. On the compatibility of a new expression for gross conversion efficiency with the Von Bertalanffy growth equation. Fish. Bull. U.S. **85**: 139–140.

Stewart, D.J., and Binkowski, F.P. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Trans. Am. Fish. Soc. **115**: 643–661.

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Stewart, D.J., and Ibarra, M. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. Can. J. Fish. Aquat. Sci. **48**: 909–922.

Stewart, D.J., Kitchell, J.F., and Crowder, L.B. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. **110**: 751–763.

Stewart, D.J., Weininger, D., Rottiers, D.V., and Edsall, T.A. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. **40**: 681–698.

Tandler, A., and Beamish, F.W.H. 1979. Mechanical and biological components of apparent specific dynamic action in largemouth bass, *Micropterus salmoides* Lacépède. J. Fish Biol. **14**: 343–350.

Tytler, P. 1969. Relationship between oxygen consumption and swimming speed in the haddock, *Melanogrammus aeglefinus*. Nature (London), **221**: 274–275.

Trippel, E.A., and Harvey, H.H. 1989. Missing opportunities to reproduce: an energy dependent or fecundity gaining strategy in white sucker (*Catostomus commersoni*)? Can. J. Zool. **67**: 2180–2188.

Ursin, E. 1967. A mathematical model of some aspects of fish growth, respiration, and mortality. J. Fish. Res. Board Can. **24**: 2355–2390.

Ursin, E. 1979. Principles of growth in fishes. Symp. Zool. Soc. London, **44**: 63–87

Van Winkle, W., Shuter, B.J., Holcomb, B.D., Jager, H.I., Tyler, J.A., and Whitaker, S.Y. 1997. Regulation of energy acquisition and allocation to respiration, growth and reproduction: simulation model and example using rainbow trout. *In* Early life history and recruitment in fish populations. *Edited by* R.C. Chambers and E.A. Trippel. Chapman & Hall, London. pp. 103–137.

Verhulst, P.F. 1838. Notice sur la loi que la population suit dans son accroissement. Corresp. Math. Phys. **10**: 113–121.

Von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. **32**: 217–231.

Ware, D.M. 1982. Power and evolutionary fitness of teleosts. Can. J. Fish. Aquat. Sci. **39**: 3–13.

Ware, D.M., and Tanasichuk, R.W. 1989. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. **46**: 1776–1784.

Waterlow, J.C. 1995. Whole-body protein turnover in humans, past, present, and future. Annu. Rev. Nutr. **15**: 57–92.

Winberg, G.G. 1956. Rate of metabolism and food requirements of fishes. Nauchn. Tr. Beloruss. Gos. Univ. Im. V.I. Lenina. (Translated from Russian by Fish. Res. Board Can. Transl. Ser. No. 194, 1960.)

Wootton, R.J., and Evans, G.W. 1976. Cost of egg production in the three-spine stickleback (*Gasterosteus aculeatus*). J. Fish Biol. **8**: 385–395.

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